# Pupilloid Land Snails from the South and Mid-west Coasts of Australia

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## ABSTRACT

Pupilloid land snails found in the areas between Kangaroo Island, South Australia and Albany, Western Australia, and then from the Chichester Range and Port Hedland in the Pilbara and North West Cape south to near Morawa, Western Australia are reviewed. Gastrocopta margaretae (Cox, 1868) (+ bannertonensis Gabriel, 1930 and complexa Iredale, 1939) ranges from the Lower Murray River basin of Victoria and South Australia west to near Merredin and Albany, Western Australia; G. wallabyensis (Smith, 1894) is known from coastal and island localities in Western Australia from Point Quobba, north of Carnarvon south through Shark Bay and the Houtman Abrolhos to Green Head, just south of Eneabba; G. pilbarana, new species, has been collected from the Chichester Range near Roy Hill Station, the North West Cape, and places in the Shark Bay area (Salutation and Dirk Hartog Islands, Useless Bay); G. deserti Pilsbry, 1917, a species widely distributed in the Red Centre and barely reaching the south fringes of the Kimberley, has been found near the North West Cape south to Point Quobba north of Carnarvon. Pupilla (Gibbulinopsis) australis (Adams & Angas, 1864) (+ lincolniensis Cox, 1867 and occidentalis Iredale, 1939) ranges from at least as far east as Kangaroo Island, South Australia, then from at least Nundroo in South Australia west to Peak Charles inland and coastally at Bremer Bay and Albany along the south coast of Western Australia, with isolated records from Rottnest Island, two islands in the Houtman Abrolhos, Green Head, and Point Quobba, north of Carnarvon on the west coast. The sinistral Pupoides myoporinae (Tate, 1880) is known from scattered localities along the south coast from the Murray River in Victoria west to Hines Hill near Merredin in the WA wheat belt; its west coast analog, P. contrarius (E.A. Smith, 1894), has been collected between N of Pardoo in the Pilbara south to the Houtman Abrolhos. Of the dextral species, Pupoides adelaidae (Adams & Angas, 1864) (+ contexta Iredale, 1939 and asserta Iredale, 1939) ranges from Victoria through South Australia as far west as Jerdacuttup, Beaufort Inlet, and Peak Charles near the south coast, Hines Hill and Nangeenan in the central wheat belt, and Nugadong and Morawa NE of Perth. P. lepidulus (Adams & Angas, 1864) ranges from Cape Latouche-Treville south to the Houtman Abrolhos. Specimens possibly referable to the Red Centre P. beltianus (Tate, 1894) or the south coast P. adelaidae, have been collected at a few stations between Dale's Gorge in the Hamersley Range, Pilbara and the Overlander Roadhouse near Shark Bay. No pupilloid snails have been recorded on the mainland between Nugadong and Morawa south to Cape Leeuwin on the west coast and then east to near Albany on the south coast of Western Australia. Hines Hill and Nangeenan near Merredin are the westernmost inland localities. Pupilloids are absent from the denser forests of south-western Australia.

The multiple thickenings of the shell lip in these species suggests considerable longevity, although, because of the variable rainfall patterns, it is doubtful that these represent annual depositions.

## INTRODUCTION

During preparation of a monograph reviewing the non-camaenid land snails of the Kimberley, Northern Territory above the Roper River, and Red Centre (Solem, In preparation), the pupilloid materials from South Australia and Western Australia below the De Gray River were reviewed. Most of these specimens were collected during field work along the south coast between Norseman, Western Australia and Nundroo, South Australia in June 1979 (WA-481 through WA-546) with Fred and Jan Aslin, Mount Gambier, South Australia. Less extensive collections from as far north as Port Hedland and as far east as Balladonia had been made by A. Solem and L. Price in January and February 1974 (WA-1 through WA-99), and a critical collection at Point Quobba (WA-167A) was made by L. Price and Carl Christensen in April 1977. Loan of pupilloids in the collection of the Western Australian Museum, Perth through the courtesy of Shirley Slack-Smith provided critical materials from south-western Western Australia and the Pilbara region.

When combined with the Kimberley-Northern Territory-Red Centre report (Solem, In preparation), the pupilloid fauna of the western two-thirds of Australia will have been summarized. While there has been adequate material from most of Western Australia and the Northern Territory to delineate at least approximate ranges, specimens available to me from the Eyre Peninsula and south-eastern South Australia were few in number. Many systematic and distributional problems relating to these areas remain to be solved.

Little information had been recorded previously on the land snails from these regions. The early descriptive papers, such as Adams & Angas (1864a, 1864b), were summarized by E.A. Smith (1894) for Western Australia. The Horn Expedition reports by Tate (1894, 1896) are still the standard account of Red Centre taxa. Later works, such as the Western Australian check list (Hedley, 1916), a check list of all land snails from Australia (Iredale, 1937a), a synoptic review and listing of both the Red Centre and South Australian taxa (Iredale, 1937b) and a more formal review of the Western Australian fauna (Iredale, 1939), essentially complete the sparse literature record. A significant defect of Iredale's work was his tendency to automatically assume that anything Australian must be at least generically distinct. More has been published on the Kimberley fauna, especially in recent years (see Solem, In preparation). Nothing has been published on the land snails of the Northern Territory above the Roper River.

Further to the east, the very competent summations of the land molluscs of Victoria by Gabriel (1930, 1947) have been greatly expanded and incorporated into a field guide for the entire southeast by B.J. Smith & Kershaw (1979). But even the last work is based on limited material from the semi-arid areas of Victoria and South Australia.

Measurements of specimens cited in this report were taken with an ocular micrometer and then converted into millimeters. Accuracy is within 0.05mm. For variable species, such as *Pupilla* (*Gibbulinopsis*) australis (Adams & Angas, 1864), all full adults were measured. For less variable species, such as *Pupoides adelaidae* (Adams & Angas, 1864), where vast numbers of individuals were available, only part of the material was measured because of time limitations. A detailed review of local variation, using degree of lip thickening and number of lip layers to estimate age classes of adults, would yield significant knowledge of local variation and permit better estimates of variability. This is thus an introductory study.

A second limitation to this report is that it is based on conchological criteria only. No data have been recorded previously concerning the anatomy of any Australian pupilloids. Preserved examples

of most taxa were available, but the time needed to initiate a comprehensive anatomical review was not. This aspect, of necessity, has been left to others. In the absence of such data, a conservative view of classification has been adopted. Whereas Iredale (1939: 6-12) split them among three families and placed all species in endemic Australian genera, I have retained the broader generic concepts of monographers. There are no conchological features that justify generic separation of the Australian pupilloids. They are very similar to species from such diverse areas as South Africa, the Mascarene Islands, Indonesia, and Bismarck Archipelago. Retention in broadly based genera gives a much better indication of possible affinities than splitting into pseudo-endemic generic units.

## ACKNOWLEDGEMENTS

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The following abbreviations indicate the depository of listed materials:

- AM Australian Museum, Sydney
- BMNH British Museum (Natural History), London
- FMNH Field Museum of Natural History, Chicago
- RNHL Rijksmuseum van Natuurlijke Histoire, Leiden
- SAM South Australian Museum, Adelaide
- SMF Forschungsinstitut Senckenberg, Frankfurt a.-M., Germany
- WAM Western Australian Museum, Perth

The number of specimens in each lot is listed after the catalog number of the lot, *i.e.*, FMNH 214235/26 indicates that there are 26 specimens in that lot.

All SEM photographs were taken by the author, using the Cambridge S4-10 Stereoscan provided Field Museum of Natural History through the support of NSF Grant BMS 72-02149. The prints were prepared by the Division of Photography, Field Museum of Natural History and mounted for reproduction by Associate Dorothy Karall and Illustrator Linnea Lahlum.

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## SYSTEMATIC REVIEW

Use of a single family Pupillidae follows Pilsbry (1948:868-1,018), rather than the division into several families presented by Zilch (1959-1960:146-173).

The following key is artificial and without phylogenetic meaning.

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## Key to the species of Pupillidae

1.	Aperture with several lamellar barriers (Figs 1-20)2 Aperture with one to four nodular barriers (Figs 21-36)5	
2.	Columellar barrier large, parallel to coiling (Figs 1-12)	
3.	Barriers smaller (Figs 1-10); southern areas Barriers much larger (Figs 11-12); mid-west coast <i>Gastrocopta margaretae</i> (Cox, 1868) 1894)	
4.	Anterior end of columellar barrier slanted downwards (Fig. 13); palatal wall with two nodular barriers (Fig. 14).Gastrocopta deserti Pilsbry, 1917Posterior portion of columellar barrier curved downward (Fig. 17); palatal wall with three large barriers (Figs 16-17, 20)Gastrocopta pilbarana, new species	
5.	Shell with sinistral coiling	
6.	Two or three deeply recessed, nodular barriers present (Figs 21-24); apex strongly rounded <i>Pupilla (Gibbulinopsis) australis</i> (Adams & Angas, 1864 Only a small angular barrier at the palatal lip margin (Figs 25-36); apex tapering	
7.	South part of Western Australia east to Victoria West coast, Pilbara south to Houtman Abrolhos Pupoides contrarius (E.A. Smith, 1894)	
8.	From south of Geraldton, WA east to Victoria; shell large Pupoides adelaidae (Adams & Angas, 186	
	West coast, Cape Latouche-Treville south to Houtman Abrolhos	
9.	Shell slender (Fig. 34)Pupoides lepidulus (Adams & Angas, 1864)Shell more obese (Figs 32, 36)Pupoides aff. beltianus, P. aff. adelaidae	
	1.24	

## **Family Pupillidae**

Three subfamilies are found in Australia. The Nesopupinae are represented in northern Australia by the genera *Pupisoma* Stoliczka, 1873 and *Nesopupa* Pilsbry, 1900 (Solem, In preparation). The Australian Gastrocoptinae consist of *Gastrocopta* Wollaston, 1878, which ranges throughout most of Australia, *Gyliotrachela* Tomlin, 1930, which occurs in scattered limestone localities across northern Australia (Solem, 1981), and a new genus with Indonesian representatives (Solem, In preparation). The Pupillinae includes *Pupilla* Leach, 1828, which ranges from near Sydney and the east coast of Tasmania across southern Australia and then up the west coast to north of Carnarvon, *Pupoides* Pfeiffer, 1854, which ranges over much of Australia, and *Glyptopupoides* Pilsbry, 1926, which is confined to eastern Queensland and the NE tip of New South Wales.

#### Subfamily Gastrocoptinae

Only members of the genus Gastrocopta are found in the area reviewed in this study.

#### Genus Gastrocopta Wollaston, 1878

In his classic monograph of this complex, Pilsbry (1916-1918:6-172) utilized a broadly defined genus *Gastrocopta* Wollaston, 1878 that was split into a number of subgenera and sections. The Australian species were placed in two subgroups:

*Sinalbinula* Pilsbry, 1916 with a palatal callus, parietal lamella straight inside or curving toward columella, the columellar barrier horizontal or the inner end curved downward. Type species: *Gastrocopta armigerella* (Reinhardt, 1877) from Japan.

Australbinula Pilsbry, 1916 without a palatal callus, parietal curving toward the columella within, angular and parietal diverging in front, columellar barrier steeply running upward within. Type species: *Gastrocopta rossiteri* (Brazier, 1877) from New South Wales.

The more material that is examined, the less the distinction between these groups can be defended. *Gastrocopta margaretae* (Cox, 1868), *G. wallabyensis* (E.A. Smith, 1894), and *G. pilbarana*, new species could be placed in *Sinalbinula* on the basis of the columellar barrier, although not fully agreeing in other features, while *G. deserti* Pilsbry, 1917 would belong to *Australbinula* despite its reduced palatal barriers. Iredale (1937a:301-302; 1937b:9-11; 1939:7-9) elevated *Australbinula* to generic rank, giving an illusion of non-relationship to external species. No subgenera are used because of these difficulties.

# Gastrocopta margaretae (Cox, 1868)

(Figs 1-10)

Pupa margaretae Cox, 1868, Monog. Aust. Land Shells, p. 80, pl. 14, figs 20, 20a — Wallaroo, South Australia.

Gastrocopta margaretae (Cox), Pilsbry, 1917, Man. Conch., (2) 24:160-161, pl. 26, figs 7-8.

Bifidaria bannertonensis Gabriel, 1930, Proc. Royal Soc., Victoria, 43 (1):64, pl. 3, figs 9-10 — Bannerton, Victoria (A.C. Nilson!).

Australbinula margaretae (Cox), Iredale, 1937, Aust. Zool., 8 (4):302; Iredale, 1937, South Aust. Nat., 18 (2):11, pl. 1, fig. 4 — rocky slopes of Mannum Cliffs, South Australia.

Australbinula complexa Iredale, 1939, Jour. Roy. Soc. Western Aust., 25:7-8, pl. 1, fig. 7 – Nangeenan, near Merredin, Western Australia.

Gastrocopta (Australbinula) margaretae (Cox), B.J. Smith & Kershaw, 1979, Field Guide to Non-Marine Molluscs of South Eastern Australia, pp. 104-5, 263, fig., map.

Gastrocopta (Australbinula) bannertonensis (Gabriel), B.J. Smith & Kershaw, 1979, Field Guide to Non-Marine Molluscs of South Eastern Australia, pp. 105, 263, fig.

#### **Comparative remarks**

Gastrocopta margaretae (Cox, 1868) is easily separated from other pupilloid genera by the presence of several slender, lamellar barriers within the aperture (Figs 1-10). Pupoides species have only a palatal notch formed by a weak angular and the palatal lip (Figs 25-28), while Pupilla (Gibbulinopsis) australis (Adams & Angas, 1864) differs in its sinistral coiling and presence of deeply recessed nodular barriers in the aperture (Figs 21-24). The closely related west coast species Gastrocopta wallabyensis (Smith, 1894) differs in having all barriers more massive (Figs 11-12), sometimes a small infraparietal barrier, and usually both the basal and upper palatal barriers much wider than the lower palatal. G. deserti Pilsbry, 1917 has the columellar barrier slanting downwards, the angular barrier greatly reduced in size, lacks the basal barrier, and has both palatal barriers small in size (Figs 13-15). G. pilbarana, new species, has three parietal barriers, the columellar barrier with its posterior portion reflected downwards, a narrow, sinuated lower palatal barrier, and both the basal and upper palatal barrier, and both the basal and upper palatal barriers.

## Material

Victoria: Bannerton (FMNH 117024/3 ex C.J. Gabriel, SAM D15592, paratypes of *Bifidaria* bannertonensis Gabriel, 1930).

South Australia: South Flinders (SA-28, Merna Mora Homestead, FMNH 211580/1); Gawler Ranges (FA-8, Mt. Ive Homestead, FMNH 212546/1); Arno Bay (salt swamps, RNHL, D. Smits!); Yorke Peninsula (Wallaroo, SMF 112500, SMF 55236, cotypes and lectotype of *Pupa margaretae* Cox, 1868, BMNH ex Beddome, cotypes of *Pupa margaretae* Cox, 1868); Eyre Peninsula (SA-8A, Mt. Young, ca 10 km SW of Whyalla, FMNH 211508/1; FA-30, Tooligie Hill, SE of Murdinga, FMNH 212638/3); Nuyts Archipelago (Fenelon Island, N. Coleman!, AM, WAM); Nullarbor area [WA-515, Brown's Hill, Nundroo, FMNH 204355/1; WA-516, 2 km E of Yalata turnoff, FMNH 204365/1; WA-511, Murrawijinie Cave (N-7), NNW of Nullarbor, FMNH 204344/15; WA-505, Clay Dam Cave (N-16), SSE of Koonalda, FMNH 204310; WA-510, Wigunda Cave (N-147), SSW of Wigunda Tanks, FMNH 204337/38; WA-520, doline (N-148), WNW of Nullarbor, FMNH 204384/2; WA-508, Koonalda Cave (N-4), N of Koonalda, FMNH 204319/8; WA-504, Allen's Cave (N-145), E of Eucla, FMNH 204297/6; WA-509, 700 m WNW of Wigunda microwave tower, SE of Koonalda, FMNH 204331/1].

Western Australia: Nullarbor and Eyre Highway area [WA-499, rim of Webubbie Cave (N-2), WNW of Eucla, FMNH 204246/4, FMNH 204247/3; WA-502, Kutowalla doline (N-44), W of Eucla, FMNH 204273/1, FMNH 204274/1; WA-503, Winbirra Cave (N-45), W of Eucla, FMNH 204287/13, FMNH 204288/1; WA-500, rim of Chowilla landslip (N-17), WNW of Eucla, FMNH 204261/1; WA-529. Forrest Road, 31.8 km N of Mundrabilla Homestead, FMNH 204440/1; WA-532, Old Homestead Cave (N-83), 39 km S of Forrest, FMNH 204450/6; WA-497, Mundrabilla microwave tower, FMNH 204230/1, FMNH 204231/2; WA-534, Forrest track, 9.8 km N of Mundrabilla Homestead, FMNH 204458/1; WA-525, W of Yakcoorga Rockhole, E of Mundrabilla, FMNH 204415/1; WA-535, Mundrabilla Homestead, FMNH 204466/3; WA-524, Kuthala Pass, N of Mundrabilla, FMNH 204404/ 8; WA-493, W of Madura, FMNH 204198/8; WA-538, Dingo Donga sink (N-160). FMNH 204487/ 7. FMNH 204488/1; 25 miles E of Madura, RNHL, G.F. Mees!, 7 February 1975; WA-537, Moodini Pass, E of Madura, FMNH 204480/6, FMNH 204481/1; WA-494, Madura 6 Mile South Cave (N-62), S of Madura, FMNH 204207/1; WA-491, N-91 Cave, E of Cocklebiddy, FMNH 204186/1; WA-490B, W side, Cocklebiddy Cave (N-48), W of Cocklebiddy, FMNH 204178/2; WA-489, 5.9 km E of Caiguna, FMNH 204165/2; Caiguna, RNHL, G.F. Mees!, 7 February 1975; WA-539, 33.4 km W of John Eyre Hotel, Caiguna, FMNH 204498/3; WA-540, 64.5 km E of Balladonia, FMNH 204520/ 1; Balladonia, RNHL, G.F. Mees!, 8-9 February 1975; WA-543, N of Juranda Rockhole, Balladonia-Cape Arid track, FMNH 204552/1; WA-485, Fraser Range Homestead, ca 103.8 km E of Norseman, FMNH 204121/5]; Recherche Archipelago (N Twin Peaks Island, 9-10 May 1976, WAM 545.76/8, WAM 546.76/3, WAM 547.76/10, WAM 548.76/15, WAM 551.76/1; E side Mondrain Island, 6 May 1976, WAM 544.76/3, WAM 549.76/2, WAM 550.76/1); Esperance (WA-546, Cape Le Grand, FMNH 204568/2; between Civic Centre and Shire Offices, 21 May 1983, WAM 187.86/3); Norseman area and south-west (Beacon Hill, Norseman, 2 January 1977, WAM 14.86/20; Steddy's Road, Grass Patch, 12 August 1976, WAM 142.86/4; Peak Charles, 16 April 1976, WAM 619.76/1, WAM 620.76/1, WAM 621.76/2, WAM 622.76/3; NNW of Peak Eleanora, 17-18 January 1977, WAM 1266.81/2); Ravensthorpe area (22.5 km W of Jerdacuttup, 17 February 1976, WAM 131.84/1); Albany area (Normans Beach, 33 km E of Albany, 3 December 1974, WAM 114.86/16, 26 March 1978, WAM 122.86/4; Betty's Beach, E of Albany, 4 December 1974, WAM 149.86/4); Kalgoorlie (Mt. Shea, NE side, 20 km SSE of Kalgoorlie, 15 March 1981, WAM 181.86/1; Merredin area (WA-98, townsite reserve, Nangeenan, W of Merredin, AMC. 64895, holotype of Australbinula complexa Iredale, 1939, WAM 117.79/2, FMNH 182230/n, FMNH 200490/14, FMNH 201531/n, topotypes of Australbinula complexa Iredale, 1939; Hines Hill townsite reserve, 10 November 1968, G.W. Kendrick!, WAM/N).

#### Range

Gastrocopta margaretae (Cox, 1868) has been collected as far west as Nangeenan and near Albany, then as far inland as Mt. Shea south of Kalgoorlie, in Western Australia. It is common from the Norseman-Peak Charles-Esperance axis to Nundroo, South Australia along the Nullarbor coast. The lack of inland records east of Balladonia may reflect lack of collecting. The very few records cited here from the Gawler Ranges, Eyre Peninsula, Flinders Ranges, and lower Murray River (Mannum, South Australia and Bannerton, Victoria) will be greatly expanded elsewhere (Solem, In preparation).

#### Discussion

Pilsbry (1916-1918:161) considered *Pupa margaretae* Cox, 1868 to be a lost species, since Charles Hedley could locate no material in the Australian Museum collection. Subsequent workers (Iredale, 1937a, 1937b; B.J. Smith & Kershaw, 1979) have used the name for various South Australian populations. Discovery of type lot material in both the SMF and BMNH collections has permitted selecting a lectotype (Figs 8-9). Type or topotypic material of both *G. bannertonensis* (Gabriel, 1930) (Fig. 10) and *G. complexa* (Iredale, 1939) (Figs 1-2) agree in all apertural features and these species are synonymized with *G. margaretae*.

The range delineated here for *Gastrocopta margaretae* probably is realistic for the western limits reached in Western Australia, roughly Merredin in the wheat belt south to Albany. No significant collections for land mollusks have been made between Nundroo and the westernmost Gawler Ranges in South Australia. Records for the Eyre Peninsula and Gawler Ranges are sparse. There are a number of records for the South Flinders Ranges. In the North Flinders it is replaced by *Gastrocopta deserti* Pilsbry, 1917. While the material available confirm the synonymy of *margaretae*, *bannertonensis*, and *complexa*, the specimens from Eastern States are not adequate to circumscribe the eastern limit of distribution. B.J. Smith & Kershaw (1979:103-104, map 40) report this from central eastern from any dense forest areas in south-western Western Australia.

Variation in barrier prominence is considerable (Figs 1-10). Generally the angular is slightly smaller than the parietal, and this is seen in all type material (Figs 1-2, 8-9, 10). In some examples (Figs 3-4) the angular is greatly reduced, but other specimens in the same population (Figs 5-7) are intermediate in character. Similarly, the width and prominence of the basal and upper palatal barriers (Figs 2, 4, 6, 7, 10) are quite variable, again more on an individual than a population basis.

Size variation is relatively minor. The cotypes of *bannertonensis* from Victoria (Fig. 10) and most of the westernmost specimens from Nangeenan near Merredin, WA (topotypes of *complexa* Iredale, 1939) are in the 2.5 to 2.9 mm height range. The types of *G. margaretae* measure 2.40-2.47 mm in shell height. The mean and range of 66 adults from sites throughout the range are 2.66 mm (2.11-3.03 mm). There is a dichotomy present in some lots, with high slender specimens at 2.6 to 3.0 mm, and shorter, more obese individuals (Fig. 5) at 2.3 to 2.55 mm. I could detect no differences in apertural barriers between adults of the two morphs (the individual shown in Fig. 5 has subadult barrier size) and I am assuming that only one species is represented. Drier stations, such as Mt. Young, S of Whyalla on the Eyre Peninsula; inland on the track from Mundrabilla to Forrest; and exposed limestone at Weebubbie and Cocklebiddy Caves, had mostly the small growth vectors fairly early in ontogeny. The more obese morph has the early spire widen more quickly and at a later time the growth ceases at a lower whorl count. The slender morph keeps a narrow spire width and then ceases growth at a higher whorl count.

In some specimens, the barrier size approaches that found in *G. wallabyensis* (E.A. Smith, 1894). These individuals, such as the lectotype of *margaretae* (Figs 8-9), show the widened basal and upper palatal barriers, but never the infraparietal found in the former species. There also is a clear indication of multiple layers on the lip itself. *Gastrocopta tatei* Pilsbry, 1917 from the Red Centre also is related, but differs in having the angular barrier extend further anteriorly, possessing an infraparietal barrier, and has more rounded whorls (Solem, In preparation). The three species probably will prove to be closely related. Presently available collections suggest that they are distinct.

## Gastrocopta wallabyensis (E.A. Smith, 1894)

(Figs 11-12)

Pupa wallabyensis E.A. Smith, 1894, Proc. Malac. Soc. London, 1 (3):97 — East Wallaby Island, Houtman Abrolhos (J.J. Walker!).

Bifidaria wallabyensis (E.A. Smith), Hedley, 1916, Jour. Roy. Soc. Western Aust., 1:217. Gastrocopta wallabyensis (E.A. Smith), Pilsbry, 1917, Man. Conch., (2) 24:171-172. Australbinula wallabyensis (E.A. Smith), Iredale, 1939, Jour. Roy. Soc. Western Aust., 25:7.

### **Comparative remarks**

Gastrocopta wallabyensis (E.A. Smith, 1894) differs most obviously from the south coast *G. margaretae* (Cox, 1868) in having more massive apertural barriers (compare Figs 1-10 and 11-12), the angular barrier is close to equalling the parietal in size, the basal and upper palatal barriers are much wider than the lower palatal (Figs 11-12), and it is found only along the west coast. Differences from the Red Centre species *Gastrocopta tatei* Pilsbry, 1917 will be discussed elsewhere (Solem, In preparation). *G. deserti* Pilsbry, 1917 has the columellar barrier slanted downward anteriorly, only two nodular palatal barriers, and the angular barrier is both reduced in size and extends much further anteriorly (Figs 13-15). *G. pilbarana*, new species, has the posterior portion of the columellar barrier curved downward, a sinuated lamellar lower palatal barrier, and an angled upper palatal barrier (Figs 16-20).

## Material

Western Australia: Carnarvon area (WA-167A, Point Quobba, N of Carnarvon, FMNH 200358/ 13); Shark Bay area (next to Northern Highway, N of Shark Bay turnoff, 9 September 1975, WAM 146.86/7; Carrarang Station, W side Useless Inlet, 24 August 1970, WAM 126.84/4); Houtman Abrolhos (East Wallaby Island, BMNH 1891.11.21.264, lectotype and BMNH 1891.11.21.265-9, SAM D13311, paralectotypes of *Pupa wallabyensis* E.A. Smith, 1894); Green Head, SW of Eneabba (20 November 1968, WAM 143.86/4).

#### Range

The few localities on the west coast of Western Australia between Point Quobba and Green Head, near Eneabba probably reflect lack of collecting rather than rarity of *Gastrocopta wallabyensis* (E.A. Smith, 1894).

## Discussion

Gastrocopta wallabyensis (E.A. Smith, 1894) is rather variable in barrier structure. A prominent infraparietal barrier may be present or absent (Fig. 11). The parietal and angular normally are widely separated, with the latter extending well towards the lip, but in some examples they are almost evenly truncated anteriorly. The columellar barrier is broad and slightly sinuated (Figs 11-12). Normally both the basal and upper palatal barriers are very broad, the former angled, while the lower palatal (Fig.11) is higher and narrower.

Gastrocopta margaretae (Cox, 1868), from the wheat belt and south coast of Western Australia east to the Murray Basin of Victoria, differs in having the angular barrier usually much smaller than the parietal (Figs 2-10), no infraparietal, and both the basal and upper palatal barriers small and tubercular in shape. The degree of apertural narrowing is much greater in *G. wallabyensis* (Figs 11-12) than in *G. margaretae* (Figs 1-10).

Shell height in 26 specimens was 2.09-2.89 mm (mean 2.42 mm). Thus *G. wallabyensis* is identical in size to *G. deserti* Pilsbry, 1917, making specimens with dirt-filled apertures almost impossible to identify, but distinctly larger than *G. pilbarana*, new species, and essentially the same size as *G. margaretae*.

## Gastrocopta deserti Pilsbry, 1917

(Figs 13-15)

Pupa mooreana Tate, 1896 (not E.A. Smith, 1894), Report Horn Scientific Expedition to Central Australia, 2, Zoology, p. 206 — In part.

Gastrocopta larapinta deserti Pilsbry, 1917, Man. Conch., (2) 24:170-171, pl. 30, figs 1-3 — Tempe Downs, Reedy Creek, Palm Creek, Stuart's Pass, Painta Spring, and Alice Springs in the Red Centre, Forrest River (18° 33'S, 125° 08' E), Western Australia (Richard Helms!).

- Australbinula larapinta (Pilsbry), Iredale, 1937, Aust. Zool., 8 (4):302 In part; Iredale, 1937, South Aust. Nat., 18 (2):10 — In part.
- Australbinula helmsiana Iredale, 1939, Jour. Roy. Soc. Western Aust., 25:8, pl. 1, fig. 2 Forrest River, Western Australia.

#### **Comparative remarks**

Gastrocopta deserti Pilsbry, 1917 is most easily recognizable in that the columellar barrier slants downward anteriorly and there are only two small barriers on the palatal wall (Figs 13-14). The angular barrier is much smaller than the parietal (Figs 13-14) and twists upward to the palatal lip edge (Fig. 15). *G. pilbarana,* new species, has three large palatal barriers, much larger parietals, and the columellar barrier has its posterior portion curved downward (Figs 16-20). Both *G. wallabyensis* (E.A. Smith, 1894) and *G. margaretae* (Cox, 1868) differ in having a simple columellar barrier that lies parallel to the coiling plane (Figs 1-12).

#### Material

Western Australia: Kimberley (Forrest River, AM C.64894, types of Australbinula helmsiana Iredale, 1939); North West Cape (Cy Creek, NE part of Cardabia Station, 6 April 1969, WAM 128.84/ 45, FMNH 215120/3); Muiron Island, 11 June 1970, K. Youngson!, WAM/8); Barrow Island (Harcourt Bay area, February 1977, H. Butler!, WAM/1); Dampier Archipelago (Dolphin Island, 19 June 1970, K. Youngson!, WAM/1); Carnarvon area (WA-167A, depression near lighthouse, Point Quobba, FMNH 201611/5).

#### Range

In the Red Centre, *Gastrocopta deserti* Pilsbry, 1917 has been collected from the Reynolds Range, NW of Alice Springs south to the Everard Range, and from the Jervois and Dulcie Ranges NE of Alice Springs to the Rawlinson and Barrow Ranges in Western Australia. There are a few confirmed records from the N Flinders Range, South Australia (Solem, In preparation). The west coast records reported here are thus surprising. This species probably lives in the interior ranges between the west coast and the Rawlinson-Warburton arcs leading to the Red Centre.

## Discussion

Despite careful comparisons, I could see no differences between the Red Centre and west coast specimens, allowing for the considerable variation in size of the angular barrier found in the former (Solem, in preparation).

The gap in records between the Rawlinson Ranges and west coast probably is an artifact caused by lack of collecting. I found only a few pupilloids in the area between the Mann Ranges and Warburton Ranges, and in the Rawlinson-Petermann arc during a hurried visit in 1984. A very unusual 325 mm rain had washed out the normal accumulations of dead micro-mollusks a few weeks prior to our trip, and thus we could easily have missed other taxa. To my knowledge, no collecting for land snails has been attempted between Warburton and the Pilbara, so this remains a blank in distributional terms.

The few specimens show little size variation. Shell height for 53 adults was 2.11-2.76 mm, mean 2.41 mm.

## Gastrocopta pilbarana, new species (Figs 16-20)

## **Comparative remarks**

Gastrocopta pilbarana, new species, is characterized by having the columellar barrier curve downward posteriorly (Figs 17-18, 20), possessing a sinuated lower palatal barrier (Figs 16-20), a prominent infraparietal barrier (Figs 17-18), and both the basal and upper palatal barriers elongated laterally (Figs 17, 18, 20). The small size, shell height 1.85-2.63 mm (mean 2.13 mm) and broadly rounded apex (Figs 16, 19) also separate this species. The sometimes sympatric *G. deserti* Pilsbry, 1917 differs in having much smaller barriers (Fig. 13), the *anterior* end of the columellar barrier slanting downward (Fig. 14), only two small barriers on the palatal wall (Figs 13-14), and the angular barrier reduced to a low ridge that angles to the palatal notch (Fig. 15). The other species with three barriers on the parietal wall, *G. wallabyensis* (E.A. Smith, 1894), has a large columellar barrier (Fig. 12) that does not descend either anteriorly or posteriorly, and a simple lower palatal barriers and a simple columellar barrier (Figs 1-10).

#### Holotype

WAM 127.84, Sandy Point, Dirk Hartog Island, Shark Bay, Western Australia, Australia. 25° 43' S, 113° 04' E. Collected 29 April 1974 by W.K. Youngson. Height of shell 2.17 mm, diameter 1.05 mm, H/D ratio 2.067, whorls 4 1/2, aperture height 0.86 mm, equalling 40% of shell height.

## Paratopotypes

WAM 145.86/19, FMNH 215118/3, from the type locality.

## **Paratypes**

Western Australia: Pilbara (Chichester Range, 14 miles N from Roy Hill Homestead, 26 June 1967, George W. Kendrick!, WAM 97.86/1): North West Cape area (Cy Creek, Cardabia Station, 6 April 1969, T. Darragh & George W. Kendrick!, WAM 150.86/45, FMNH 215119/3): Warroora Station (under limestone rocks, 29 June 1972, N. Coleman!, AM C.92017/2); Shark Bay (Carrarang Station, W side Useless Inlet, 24 August 1970, A. Baynes!, WAM 147.86/9; Salutation Island, 30 August 1965, G.M. Storr!, WAM 151.86/1; ½ mile west of 512 mile peg, NW Coastal Highway, NNE of Carbla Homestead, near Hamelin Pool, 20 August 1968, WAM 148.66/1).

#### Description

Shell small, height 1.85-2.63 mm (mean 2.13 mm), cylindrical, with 4 3/8 to 4 5/8 + whorls. Apex rounded, whorls of spire only slightly increasing in width (Figs 16, 19). Sculpture mostly covered by debris, low and irregular growth ridges visible on parts of shell. Aperture subcircular, with very broadly expanded lip and well developed parietal callus (Figs 16-20). Surface of lip and barriers with micro-projections (Figs 18, 20). Parietal wall with three barriers: parietal largest, slightly curved anteriorly and expanded above (Figs 17-18, 20); infraparietal low, much shorter (Fig. 17), wider (Figs 18, 20). Columellar barrier very large (Figs 17-18, 20) with posterior portion deflected downward, but little expanded above. Basal barrier angled laterally, varying in form from bifurcate (Fig. 17)

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to simple (Fig. 20). Lower palatal high, slightly expanded above (Fig. 20), strongly sinuated posteriorly (Figs 17-18, 20). Upper palatal barrier short, angled in position, expanded above, variable in form (Figs 18, 20). Based on 73 adult specimens.

## Range

*Gastrocopta pilbarana*, new species, has been collected from 14 miles N of Roy Hill Station, Chichester Range, Pilbara south through Shark Bay, WA.

## Discussion

The New South Wales species *Gastrocopta (Sinalbinula) hedleyi* Pilsbry, 1917 (Pilsbry, 1916-1918: 166-167, pl. 27, figs 1-4) from Narrabri, New South Wales (30° 20' S, 149° 47' E) has similar columellar and lower palatal barriers, but differs in its unique parietal-angular barrier positioning, and smaller basal barrier. Its type locality lies in the Upper Darling drainage on the lower west slopes of the Great Dividing Range. Probably *G. hedleyi* and *G. pilbarana* are closely related, even though on opposite sides of Australia.

Despite the fairly extensive range, specimens of *G. pilbarana* showed only minor size variation. The mean and ranges of the samples are:

LOCALITY	SPECIMENS	MEAN AND RANGE OF HEIGHT IN MM
Cy Creek	48	2.11 (1.85-2.53)
Dirk Hartog Is.	17	2.09 (1.85-2.53)
Carrarang Station	5	2.30 (2.17-2.40)

Most specimens from Cy Creek had the apertures clogged with dirt and thus variation in barriers was not checked. The illustrated Dirk Hartog examples (Figs 16-20) indicate the barrier variation within this population. Additional examples from Monajee Cave, Cape Range (WAM 71.990, WAM 71.999, WAM 71.1006, WAM 71.1010, WAM 71.1017) and WAM Cave I (WAM 65.484) were seen after the description was prepared.

## **Subfamily Pupillinae**

Of the three Australian genera, only Glyptopupoides does not occur in this region.

## Genus Pupilla Leach (in Fleming), 1828

The last world monograph of this genus, Pilsbry (1920-1921:152-225), recognized 35 recent species, divided among four sections.

The following names have been used as subgenera, sections, or genera for the Australian species. They apply to the same morphotype within the genus *Pupilla*.

Gibbulinopsis Germain, 1919, Bull. Museum Hist. Nat., Paris, 25:265 — type species Pupa pupula Deshayes, 1863.

Primipupilla Pilsbry, 1921, Man. Conch., (2) 26:153 — type species Pupa signata Mousson, 1873.

Omegapilla Iredale, 1937, Aust. Zool., 8 (4):304 — type species Pupa nelsoni Cox, 1864; Iredale, 1937, South Aust. Nat., 18 (2):14; Iredale, 1939, Jour. Roy. Soc. Western Australia, 25:12.

Although Iredale separated the Australian species into an endemic genus, *Omegapilla*, stating that "I reiterate my conclusion that the association of southern Australian Pupoids with those from Europe and South Africa is basically unsound, and should not be recognized by Australian conchologists" (Iredale, 1939:12), he cited no differentiating features. Until a revision of the *Pupilla* from the Mascarene islands and South Africa can be undertaken and comparisons made with the anatomy of Australian morphs, nothing is gained by generic endemicity. There are no conchological features suggesting such differentiation, and no anatomical studies have been made on species belonging to any of these faunas. In the absence of known differentiating features, they are kept associated with *Pupilla*.

There also has been little appreciation of the variability found within and among populations of *Pupilla*. Rousseau & Laurin (1984) analyzed variation in populations of the European *Pupilla* 

muscorum (Linnaeus, 1758), demonstrating allochronic shifts in size and shape as local climatic changes occurred.

Larger samples will include both smaller and larger adult shells. Presumably nearing adulthood in a wetter season results in a larger shell, growing up in a drier year results in smaller examples. Barrier size seems to be dependent upon age. Specimens with less fully reflected and thickened shell lips have smaller nodules and often lack both the angular and lower-palatal nodules. In contrast, the examples with fully reflected and thickened lips have a full complement of barriers which are larger in size. There appears to be only the one species ranging from Kangaroo Island and the Eyre Peninsula west to Rottnest Island, Houtman Abrolhos, and Point Quobba, Western Australia.

B.J. Smith & Kershaw (1979:103, 106-7, 263, map 41) cite *Pupilla australis* (Adams & Angas, 1864) as ranging through "Central and southern South Australia and western Victoria" and mention that *Pupilla nelsoni* (Cox, 1864), described from Nelson Bay, Sydney, and *Pupilla tasmanica* (Johnston, 1883), described from eastern Tasmania, are other members of this complex. Too little material from the Eastern States was available for me to comment on the synonymy of these taxa, but it is quite possible that the range of *australis* will be extended eastwards. It has been collected under rocks, either in coastal areas or in semi-desert, mallee areas (B.J. Smith & Kershaw, 1979:106).

## Pupilla (Gibbulinopsis) australis (Adams & Angas, 1864) (Figs 21-24)

- Vertigo australis Adams & Angas, 1864, Proc. Zool. Soc., London, 1863:553 Rapid Bay, (35°32'S, 138°11'E), Fleurieu Peninsula, South Australia.
- Pupa lincolniensis Cox, 1867, Proc. Zool. Soc., London, 1867:39 Port Lincoln, South Australia; Cox, 1868, Monog. Aust. Land Shells, p. 80, pl. 14, fig. 16; E.A. Smith, 1894, Proc. Malac. Soc. London, 1 (3):96 — Pigeon Island, near Wallaby Island (Dr. Richardson) and East Wallaby Island, Houtman Abrolhos (J.J. Walker), Western Australia.
- Pupa australis (Adams & Angas), Cox, 1868, Monog. Aust. Land Shells, p. 79.
- Vertigo lincolnensis (Cox), Hedley, 1916, Jour. Roy. Soc. Western Aust., 1:68.
- Pupilla australis (Adams & Angas), Pilsbry, 1921, Man. Conch., (2) 26:218-221, pl. 23, figs 13-19 in part.
- Omegapilla australis (Adams & Angas), Iredale, 1937, Aust. Zool., 8 (4):305; Iredale, 1937, South Aust. Nat., 18 (2):14.
- Omegapilla occidentalis Iredale, 1939, Jour. Roy. Soc. Western Aust., 25:12, pl. 1, fig. 10 no type locality cited.

## **Comparative remarks**

*Pupilla (Gibbulinopsis) australis* (Adams & Angas, 1864) is easily recognized because of its sinistral coiling and presence of deeply recessed basal and palatal nodules (Figs 21-24). The Red Centre *P. (G.) ficulnea* (Tate, 1894) is dextral in coiling, but otherwise very similar (Solem, In preparation). Sinistral species of *Pupoides* are easily separable in having only the weakly developed angular notch and a less rounded spire (Figs 25-36).

## Material

South Australia: Arno Bay (RNHL/2); Kangaroo Island (KI-47, Stokes Bay, FMNH 215969/24; KI-30, Cape du Couedic, FMNH 215928/21): Eyre Peninsula (FA-30, lower slope Tooligie Hill, Tooligie Range, SE of Murdinga, FMNH 212639/6; Port Lincoln, AM; Fenelon Island, Nuyts Archipelago, 10 January 1971, N. Coleman!, AM, SAM, WAM). Nullarbor Plain [WA-515, Brown's Hill, 0.5 km W of trig, Nundroo, FMNH 204358/3; WA-516, 20 km E of Yalata turn-off, SE Yalata Roadhouse, FMNH 204367/23; Ivy Tank, RNHL/n; WA-511, Murrawijinie Cave # 1 (N-7), NNW of Nullarbor, FMNH 204342/1; WA-505, Clay Dam Cave (N-16), 2 km N of Eyre Highway, SSE of Koonalda, FMNH 204309/5; WA-508, base of doline, Koonalda Cave (N-4), FMNH 204320/1; WA-504, Allen's Cave (N-145), SSE of Sixteen Mile Tank, FMNH 204296/13].

Western Australia: Nullarbor Plain [WA-499, rim of Weebubbie Cave (N-2), WNW of Eucla, FMNH 204244/4. FMNH 204245/9; WA-503 Winbirra Cave (N-45), W of Eucla, FMNH 204284/1; WA-501, rim to bottom of doline, Abrakurrie Cave (N-3), W of Eucla, FMNH 204268/2; Eucla, RNHL/

6; WA-525, scarp base W of Yakcoorga Rock Hole, E of Mundrabilla, FMNH 204414/2; WA-524, Kuthala Pass, N of Mundrabilla Roadhouse, FMNH 204405/3; WA-597, gully behind Mundrabilla micro-wave tower, E of Mundrabilla, FMNH 204228/10, FMNH 204229/5; WA-536, 10.2 km S of Eyre Highway, Roe Plains, E of Madura, FMNH 204771/1; WA-537, gully at base of scarp, Moodini Pass, E of Madura, FMNH 204482/1, FMNH 204483/4; WA-494, Madura 6 Mile South Cave (N-62), S of Madura, FMNH 204208/1; WA-538, Dingo Donga sink (N-160), WNW of Madura, FMNH 204489/1, FMNH 204490/1; WA-493, campsite 360 m N of Eyre Highway, W of Madura, FMNH 204199/24; WA-491, W rim to bottom of N-91 Cave, E of Cocklebiddy, FMNH 204187/1; WA-490B, W side, ca half way down doline, Cocklebiddy Cave, 10.4 km N of Eyre Highway, W of Cocklebiddy, FMNH 204179/1; Caiguna, RNHL/3; WA-488, scrub behind John Evre Motel, Caiguna, FMNH 204154/2; WA-539, S of Eyre Highway, 33.4 km W of John Eyre Motel, FMNH 204499/1; WA-489, 5.9 km E of Caiguna, FMNH 204166/1; WA-540, 64.5 km E of Balladonia Homestead, FMNH 204517/ 1; rest area 54 km E of Balladonia, 12 May 1985, WAM 173.86/2; WA-541, 38.3 km E of Balladonia Homestead, FMNH 204523/6; Balladonia, RNHL/7; WA-94, scrub north of Balladonia Hotel-Motel, FMNH 182326/2; Balladonia track, 42 miles S from Zanthus, 1965, WAM 157.86/1]; Norseman-Esperance-Cape Arid-Newman Rocks area (WA-543, woods just N of Juranda Rockhole, Balladonia-Cape Arid track, FMNH 204550/1, FMNH 204551/4; 15 miles SW of Balladonia, 23 October 1968, WAM 158.86/4; WA-93, 51 miles E of Norseman town centre, FMNH 182274/5; ca 1 mile E of Newman Rocks, NW of Balladonia, 23 October 1968, WAM 165.86/23; WA-546, Cape Le Grand campground, FMNH 204564/1; WA-91, Cape Le Grand road, 0.8 km E of Norseman Road junction, WAM 139.79/2, FMNH 182424/2, FMNH 182439/5; Cape Le Grand, 22 February 1967, WAM 152.86/ 1; between Civic Centre and Shire Offices, Esperance, 21 May 1983, WAM 185.86/ca 25; Peak Charles, WAM 1221.81/1, WAM 608.76/1, WAM 609.76/2; Grass Patch, N of Esperance, WAM 155.86/1, WAM 156.86/1): Bremer Bay region (3 miles E of Ravensthorpe, 19 January 1972, WAM 166.86/2; 22.5 km W of Jerdacuttup, 17 February 1976, WAM 108.86/26; Point Charles, mouth of Fitzgerald Inlet, 16 October 1974, WAM 168.86/1; Bremer Bay, 25 December 1970, WAM 167.86/ 5; Boat Harbour, Beaufort Inlet, W of Bremer Bay, 10 October 1974, WAM 153.86/4); Albany area (Herald Point, 13 km E of Albany, 5 December 1974, WAM 159.86/1; Betty's Beach, 32 km E of Albany, 3 December 1974, WAM 154.86/8; ridge just W of Limestone Ridge, Albany, 28 January 1970, WAM 160.86/1); Rottnest Island, Perth (W end Geordie Bay, 26 May 1973, WAM 163.86/ 4; limestone ridge near old salt works, 26 May 1973, WAM 162.86/3; Bathurst Point, December 1973, WAM 161.86/2, 5 August 1974, WAM 164.86/1, AM C.63664/2, syntypes of Omegapilla occidentalis Iredale, 1939); Eneabba (Green Head, 20 November 1968, A. Baynes!, WAM/5); Merredin area (Hines Hill, 10 November 1968, G.W. Kendrick!, WAM/5); Carnarvon area (WA-167a, depression in dunes near lighthouse, Point Quobba, FMNH 200360/9).

### Range

Apparently *Pupilla (Gibbulinopsis) australis* (Adams & Angas, 1864) is generally distributed in coastal and near coastal localities from Albany, Western Australia to Nundroo, South Australia. There are scattered inland records from Peak Charles, Grass Patch, Newman Rocks, 42 miles S of Zanthus, Hines Hill, and Balladonia in Western Australia. Isolated Western Australian populations are known from Rottnest Island off Perth, at least two of the Houtman Abrolhos, and at Green Head near Eneabba, and Point Quobba, north of Carnarvon on the mainland coast. The old record for Port Lincoln and the Tooligie record above are the only Eyre Peninsula records available at this time. It has not been taken in the Gawler or Flinders Ranges, but does occur on Kangaroo Island.

#### Discussion

Available adult material of *Pupilla (Gibbulinopsis) australis* (Adams & Angas, 1864) ranged in size from 2.25-3.55 mm in shell height. For 166 measured adults, the mean shell height was 2.88 mm (median 2.90 mm). About half (50.6%) of the individuals were clustered in the 2.63-2.93 mm range. There is no clear geographic pattern to shell size.

The largest individuals came from Kangaroo Island and Rottnest Island, at the opposite extremes of reported range, then Jerdacuttup and Cape Le Grand in the middle of the range. Dead specimens can be assumed to represent several year classes, and thus are not monomorphic. No statistical treatment was attempted as height distribution clearly was not normal within the larger samples. Some populations are smaller or larger than the norm, but these probably reflect local factors. The following samples give an indication of size variability:

LOCALITY	SPECIMENS	HEIGHT IN MM	MEAN HEIGHT
Rottnest Is.	9	2.67-3.49	2.92
Point Quobba	7	2.50-3.03	2.76
Jerdacuttup	15	2.63-3.32	2.98
Esperance	8	2.63-2.90	2.78
Newman Rocks	21	2.37-2.99	2.76
Tooligie, Eyre P.	7	2.57-2.96	2.72
Kangaroo Is.,	8	3.03-3.55	3.24
Stokes Bay			

The Rottnest listing comprises three separate collections.

*Omegapilla occidentalis* Iredale, 1939 is not separable from the other populations. Two specimens from Rottnest Island show the range in barrier size and shell height. The larger example, 3.52 mm high, has bigger barriers (Figs 21-23) and there are several layers deposited over the palatal lip of the shell. The smaller individual is about average in size, height 2.7 mm, and also is adult (Fig. 24), but has small apertural barriers and shows only the initial reflection and thickening of the shell lip.

## Genus Pupoides Pfeiffer, 1854

The most recent world monograph of *Pupoides* (Pilsbry, 1920-1921:108-147) recognized 28 species without subgeneric differentiation. In his last commentary on the genus (Pilsbry, 1948:920-926), he utilized a subgenus *Ischnopupoides* for those species in which the diameter was less than half the shell height, contrasted with the more obese species placed in *Pupoides, s.s.* Since this shape dichotomy occurs in most areas inhabited by *Pupoides,* it seems probable that convergence is involved.

Iredale (1930:120) proposed that the Australian species be placed in a new genus, *Themapupa*, which he used subsequently (Iredale, 1937a:303-304; 1937b:11-13; 1939:9-11). The original description was casual, stating "This species has been recently classed under *Pupoides*, a North American genus, with which it has no real relationship, so that it is here named *Themapupa*." The comment of Pilsbry (1927-1935:80) in his supplemental treatment of *Pupoides* is worth quoting:

Add to synonyms: *Themapupa* IREDALE, The Victorian Naturalist vol. 47, Nov. 1930, mt. *Pupa beltiana* Tate.

Mr. Iredale states that "it has no real relationship" with *Pupoides*, but he does not attempt to mention any differential character in the half page treating of "*Themapupa*" *beltiana*. Until such characters are indicated, there seems little reason to regard *Themapupa* seriously.

The only non-Iredalean literature references are Zilch (1959-1960:168) who used *Themapupa* as a subgenus of *Pupoides*, and B.J. Smith & Kershaw (1979:107-108, 263), who returned to the name *Pupoides*.

Although *Themapupa* is nomenclaturally available, until differentiating characters are discovered, it should be placed as a synonym of *Pupoides*.

The distribution of *Pupoides* is remarkable. One complex of species is common in North America and the West Indies, with a few outliers in Mexico, Peru, and Bolivia. A second complex is widely distributed in India, Sri Lanka, Afghanistan, Middle East, Egypt, Eritrea, Ethiopia, then East Africa, Cape Verde Islands south to Namibia and South Africa. Finally, there are a number of species described from the semi-arid areas of Australia. On the basis of shell features, I can see no significant differences among species from the three areas.

The literature relating to the Australian complex is confusing. There has been no agreement as to whether dextral and sinistral populations are genetic variants or distinct species. The present material suggest that distinct species are involved. Wherever a dextral and a sinistral form were microsympatric, there were noticable size and shape differences between the two morphs. If they were variants of a single species, then size and shape should be almost identical within that population. Thus I am predicting that species level differences are involved. At present, the following names, based on Australian material, are available for use:

#### SINISTRAL COILING

Pupoides myoporinae (Tate, 1880) (= Bulimus sinistrorsus Tate, 1879, not Serres, 1841) ---Peelunibie, head of Great Australian Bight.

Pupoides contrarius (E.A. Smith, 1894) — East Wallaby Island, Houtman Abrolhos.

Pupoides ischnus (Tate, 1894) — Alice Springs and Palm Creek, Red Centre,

Pupoides eremicolus (Tate, 1894) — Central Australia.

Pupoides pacificus var. sinistralis Pilsbry, 1921 — Cassini Island, Western Australia.

## DEXTRAL COILING

Pupoides pacificus (Pfeiffer, 1846) — Sir Charles Hardy's Island, Queensland. Pupoides adelaidae (Adams & Angas, 1864) (= Pupa ramsayi Cox, 1864) — South Australia. Pupoides lepidulus (Adams & Angas, 1864) — Shark Bay, Western Australia. Pupoides beltianus (Tate, 1894) - Central Australia. Pupoides anapacificus (Iredale, 1939) — Forrest River, Kimberley, Western Australia. Pupoides diruptus (Iredale, 1939) — Napier Range, Western Australia. Pupoides beltianus contextus (Iredale, 1939) — Čardanumbi, Western Australia. Pupoides beltianus assertus (Iredale, 1939) — Nangeenan near Merredin, Western Australia. Pupoides compertus (Iredale, 1940) - Collarenebri, New South Wales. Pupoides amolitus (Iredale, 1940) — Broken Hill, New South Wales.

There are thus 15 available names. The older ones have been used in a variety of contexts over the years. Sorting out the various citations from older literature is a task for historians, possible only by rediscovering the material on which that record was based. The abundant material available for this study suggests that there are a few recognizable geographic species clusters, and a series of currently unsolvable puzzles on the mid-west coast of Western Australia. These are outlined and names attached in order to provide a better framework for future revisions. The Kimberley and Red Centre taxa will be reviewed elsewhere (Solem, In preparation).

The sinistral morphs are grouped as follows:-

Pupoides myoporinae (Tate, 1880)

From Hines Hill and Nangeenan, Western Australia east to the Eyre and Yorke Peninsulas and to Bannerton, Victoria.

Pupoides contrarius E.A. Smith, 1894

From Houtman Abrolhos north to Hermite Island, Monte Bello Islands, Port Hedland, 36 miles NE of Pardoo, Western Australia, and Cape Latouche-Treville, SW of Broome.

Pupoides ischnus (Tate, 1894)

Red Centre (Solem, In preparation)

Pupoides eremicolus (Tate, 1894)

Red Centre (Solem, In preparation)

The dextral morphs are tentatively grouped as follows:

Pupoides adelaidae (Adams & Angas, 1864) (+ contextus and asserta Iredale, 1939, amolita Iredale, 1940) Lower Murray River in Victoria west to Ravensthorpe area, Hines Hill near Merredin in the wheat belt, and as far north as Morawa, NNE of Perth, WA

Pupoides lepidulus (Adams & Angas, 1864)

Houtman Abrolhos to North West Cape and Cape Latouche-Treville, SW of Broome Pupoides aff. beltianus (Tate, 1894)

Overlander Roadhouse and Shark Bay north to Dale's Gorge, Hamersley Range

Pupoides aff. adelaidae (Adams & Angas, 1864)

Shark Bay to North West Cape

The sinistral species are reviewed first.

# Pupoides myoporinae (Tate, 1880)

(Figs 25-26)

Bulimus sinistrorsus Tate, 1879 (not Serres, 1841), Trans. Proc. Phil. Soc., Adelaide, 1878-9:134, pl. 5, fig. 4 — Peelunibie, Head of the Bight, South Australia (ca 31°29'S, 131°07'E).

Bulimus myoporinae Tate, 1880, Trans. Proc. Roy. Soc., South Aust., 3:104 — New name for B. sinistrorsus Tate, 1879 (not Serres, 1841).

Pupoides myoporinae (Tate), Pilsbry, 1921, Man. Conch., (2) 26:146, pl. 15, fig. 6.

Themapupa myoporinae (Tate), Iredale, 1937, Aust. Zool., 8 (4):304; Iredale, 1937, South Austr. Nat., 18 (2):13.

## **Comparative remarks**

*Pupoides myoporinae* (Tate, 1880) is relatively large, sinistral, shell height 4.18-5.29 mm (mean of 79 adults is 4.68 mm), slender, and with rounded whorls (Figs 25-26). *P. ischnus* (Tate, 1894) from the Red Centre is even more slender, somewhat smaller in size (shell height of 26 adults 3.92-4.77 mm, mean 4.26 mm), and with the whorls flatter in shape (Fig. 29). *P. eremicolus* (Tate, 1894) from the Red Centre is larger (shell height of 51 adults 4.56-6.54 mm, mean 5.14 mm), much more obese, and with well rounded whorls (Fig. 30). The Western Australian *P. contrarius* (E.A. Smith, 1894) is dimorphic in size, generally more obese, and similar in whorl contour (Figs 27-28). Dextral taxa differ most obviously in their mode of coiling.

## Material

Victoria: Lower Murrary River (Bannerton, November 1928, A.C. Nilson, FMNH 117032/3 ex C.J. Gabriel).

South Australia: Peelunibie, head of Great Australian Bight (SAM D15563, holotype of *Bulimus sinistrorsus* Tate, 1879, SAM D3048, paratypes, AM C.60459/3, AM/3, AM/3); Nullarbor Plain (WA-516, 2 km E of Yalata turnoff, Eyre Highway, FMNH 204364/9; WA-504, Allen's Cave (N-145) doline (N-146), SSE of Sixteen Mile Tank, FMNH 204299/1).

Western Australia: Nullarbor Plain (WA-537, gully at base of scarp, Moodini Pass, FMNH 204479/ 1; WA-493, 360 metres N of Eyre Highway, W of Madura, FMNH 204196/15; WA-540, 64.5 km E of Balladonia Homestead, FMNH 204518/1; WA-541, 38.3 km E of Balladonia, FMNH 204522/ 4): Norseman-Esperance-Balladonia area (WA-94, scrub N of Balladonia Motel, FMNH 182443/1; WA-543, Juranda Rockhole, Balladonia-Cape Arid track, FMNH 204549/1; 18 km NE of Charlina Rocks, 15 October 1977, WAM 1248.81/1; 1 mile E of Newman Rock, 23 October 1968, WAM 138.86/2; Beacon Hill, Norseman, 2 January 1977, WAM 137.86/13; Peak Charles, 16 April 1976, WAM 633.76/1); Kalgoorlie area (NE side Mt. Shea, 20 km SSE of Kalgoorlie, 15 March 1981, WAM 183.86/13; Mt. Jackson, 14 April 1980, WAM 1222.81/3): Merredin area (Hines Hill townsite reserve, 10 November 1968, WAM 104.86/30).

## Range

*Pupoides myoporinae* (Tate, 1880) has an apparently disjunct range, with an eastern pocket extending from the Eyre Peninsula to Bannerton, Victoria, and then a western zone from Hines Hill near Merredin, Western Australia east to Yalata in South Australia. It has not been collected inland along the trans-continental rail line.

## Discussion

Although having basically the same geographic range, *Pupoides myoporinae* (Tate, 1894) is obviously much less abundant and present at fewer localities than *Gastrocopta margaretae* (Cox, 1868), *Pupilla* (*Gibbulinopsis*) australis (Adams & Angas, 1864) or *Pupoides adelaidae* (Adams & Angas, 1864). It also is less variable in size and shows an overall normal distribution of shell height. The dextral species *Pupoides adelaidae* (Adams & Angas, 1864) occupies the same basic range, but has been found at several places inland along the trans-continental railroad line and also extends north-west from the Hines Hill termination of the other species to Morawa, NNE of Perth near the Western Australian coast.

## Pupoides contrarius (E.A. Smith, 1894)

(Figs 27-28)

Pupa contraria E.A. Smith, 1894, Proc. Malac. Soc. London, 1 (3):96 — East Wallaby Island, Houtman Abrolhos, Western Australia (J.J. Walker!).

Pupoides contrarius (E.A. Smith), Hedley, 1916, Jour. Roy. Soc. Western Australia, 1:68; Pilsbry, 1921, Man. Conch., (2) 26:144 — In part.

Themapupa contraria E.A. Smith), Iredale, 1937, Austr. Zool., 8 (4):303; Iredale, 1939, Jour. Roy. Soc. Western Australia, 25:9.

## **Comparative remarks**

Pupoides contrarius (E.A. Smith, 1894) is sinistral, smaller (mean shell height 4.02 mm) and usually with more rounded whorls (Fig. 27) than the south coast *P. myoporinae* (Tate, 1880) (mean shell height 4.68 mm) (Figs 25-26). Both sinistral Red Centre species differ considerably: *P. ischnus* (Tate, 1894) is slightly larger (mean shell height 4.26 mm) and much more slender in shape (Fig. 29), while *P. eremicolus* (Tate, 1894) is much larger (mean shell height 5.14 mm) and considerably more obese in form (Fig. 30). Dextral taxa differ most obviously in their mode of coiling.

## Material

Western Australia: Broome (Cape Latouche-Treville, Looroo Well, C. Davis!, 4 June 1943, AM/ 11; 5 miles N of Sandfire Roadhouse, WAM/2); Pilbara (Great Northern Highway, 36 miles NE Pardoo turnoff, 28 June 1967, WAM 103.86/3); Port Hedland (WA-42, ca 1 mile S of Port Hedland, FMNH 182608/14, FMNH 182732/2); Monte Bello Islands (Hermite Island, 11 December 1979, WAM 1234.81/30); Barrow Island (February 1977, WAM 100.86/11): WA-45, Onslow Road, 5.8 km NNW of Carnarvon-Roebourne Road, WAM 146.79/3, FMNH 182736/2, FMNH 182540/10); Cape Range (1964, FMNH 171636/1; WA-14, Goat Cave, WAM 141.79/4, FMNH 182688/13, FMNH 182734/2; WA-175, Goat Cave, FMNH 199438/3; WA-178, Goat Cave, FMNH 199405/2; Goat Cave, June-July 1964, FMNH 171620/2; near Cape Range # 2 oil well, 18 May 1965, WAM 132.86/23, WAM 128.86/14; Charles Knife Road, 18 June 1966, WAM 130.86/1; WA-176, 8.8 km up Charles Knife Road, FMNH 199426/1; Shothole Canyon, 19 October 1962, WAM 129.86/4; 19 km N of Point Cloates, 8 September 1968, WAM 131.86/14; WA-22, 14.9 miles N of Ningaloo Homestead, FMNH 182355/1): Cardabia Station (Cy Creek, 6 April 1968, WAM 125.86/2; Cy Creek, 6 April 1969, WAM 127.86/5, WAM 133.84/n, FMNH 215139/5): Carnarvon area (WA-167a, depression near lighthouse, Point Quobba, FMNH 200357/12): Shark Bay (Dirk Hartog Island, 29 April 1974, WAM 133.86/10; Carrarang Station, Useless Inlet, 24 August 1970, WAM 135.86/4): Houtman Abrolhos (East Wallaby Island, syntypes of Pupa contraria E.A. Smith, 1894, BMNH 1891.11.21.225-236).

## Range

*Pupoides contrarius* (E.A. Smith, 1894) has been collected from Cape Latouche-Treville, SW of Broome, south to Shark Bay and the Houtman Abrolhos Islands, Western Australia.

#### Discussion

There is considerable geographic size variation present among the populations grouped here as *Pupoides contrarius* (E.A. Smith, 1894). It is quite possible that two species are being lumped, but available material is inadequate to resolve this problem. The northern specimens, from the Onslow turnoff on the Great Northern Highway to Port Hedland and north of Pardoo, are larger than those from the Cape Range south to Shark Bay. Dwarfed individuals have been collected at Cy Creek, Cardabia Station, just S of the Cape Range. The summed measurements compare as follows:

	MEAN SHELL		
AREA	SPECIMENS	HEIGHT	RANGE
Northern	46	4.37 mm	3.46-5.16
Southern	97	3.79 mm	2.94-4.64
TOTAL	143	4.03 mm	2.94-5.16
Cy Creek	32	3.33 mm	3.14-3.66

The difference is actually more striking than indicated, since three of the northern examples were only 3.5-3.6 mm high; the other 43 were more than 4.1 mm high.

The North West Cape to Houtman Abrolhos populations are thus smaller in size than the south coast *Pupoides myoporinae* (Tate, 1894), but the northern populations are similar in size, although generally more obese in form. The only sinistral *Pupoides* recorded from the Kimberley is a population from Cassini Island, Admiralty Gulf that E.A. Smith (1894:96) recorded as *Pupoides pacificus* (Pfeiffer, 1846), Pilsbry (1921-1922:144) named "Form *sinistralis*, and Iredale (1939:9) elevated to species rank "to keep this shell under review".

The significance of the size dichotomy is uncertain. The average total rainfall increases from the

North West Cape to Port Hedland, as well as the average number of significant rains during the year. The larger northern specimens may reflect only an increase in moisture and thus larger shell size. The Cy Creek situation is discussed below.

## Pupoides adelaidae (Adams & Angas, 1864) (Fig. 31)

Buliminus (Chondrula) adelaidae Adams & Angas, 1864, Proc. Zool. Soc., London, 1863:522 — South Australia.

Pupa ramsayi Cox, 1864, Cat. Australian Land Shells, p. 28 — Point Lowly (32°50'S, 137°48'E), South Australia.

Bulimus adelaidae (Adams & Angas), Cox, 1868, Monog. Aust. Land Shells, p. 69, pl. 13, fig. 5.

Pupoides adelaidae (Adams & Angas), Pilsbry, 1921, Man. Conch., (2) 26:140-141, pl. 15, figs 1-2
— Flinders Range, Rapid Bay, Wallaroo, Point Lowly, Port Lincoln, South Australia; Gabriel, 1930, Proc. Roy. Soc. Victoria, 43 (1):64 — Irymple, Sea Lake, Mallee, Bannerton, Geelong, Victoria; B. J. Smith & Kershaw, 1979, Field Guide to the Non-Marine Molluscs of South Eastern Australia, pp. 107-108, fig, Map 42.

Themapupa adelaidae (Adams & Angas), Iredale, 1937, Aust. Zool., 8 (4):304; Iredale, 1937, South Aust. Nat., 18 (2):13.

Themapupa beltiana contexta Iredale, 1939, Jour. Roy. Soc. Western Aust., 25:11 — Cardanumbi, Western Australia (32° 17' S, 125° 36' E).

Themapupa beltiana asserta Iredale, 1939, Jour. Roy. Soc. Western Aust., 25:11 — Nangeenan via Merredin, Western Australia (E. Sedgwick!) (31° 31' S, 118° 10' E).

*Themapupa amolita* Iredale, 1940, The Australian Nat., 10:236, fig. 3 — Broken Hill (E.W. Lower!) (31° 58' S, 141° 27' E), New South Wales.

## **Comparative remarks**

Pupoides adelaidae (Adams & Angas, 1864) is characterized by its large size, shell height 4.38-6.8 mm (mean of 224 adults is 5.43 mm), dextral coiling (Fig. 32), generally reduced sculpture, and rounded whorls. Some west coast populations approach the lower part of the size range, while Pupoides beltianus (Tate, 1894) from the Red Centre is smaller and with more strongly rounded whorls. The often microsympatric Pupoides myoporinae (Tate, 1880) has sinistral coiling (Figs 25-26), is distinctly smaller, shell height 4.18-5.29 mm (mean of 79 adults is 4.68 mm), and usually has more rounded whorls.

## Material

New South Wales: Broken Hill (AM C.101062, Holotype of Themapupa amolita Iredale, 1940).

Victoria: Murray River Basin (Merbein, 34° 10' S, 142 °04' E.C. Oke!, FMNH 117033/3 ex C.J. Gabriel; Mildura, AM C.40892/2).

South Australia (FMNH 48949/4 ex W.F. Webb, FMNH 91754/4 ex Fred Button, J. Brazier, possible type lot); Gulf of St. Vincent (Hallet's Cove, FMNH 111282/4 ex W.J. Eyerdam, SAM; Arno Bay, RNHL/4); Kangaroo Island (KI-2, Alex Outlook, Dudley Peninsula, FMNH 215868/49; KI-47, Stokes Bay, FMNH 215970/13); Nuyts Archipelago (Fenelon Island, 10 January 1971, N. Coleman!, AM/ 7); Nullarbor Plain [WA-515, Brown's Hill, Nundroo, FMNH 204356/2, FMNH 204357/2; WA-516, 2 km E of Yalata turnoff, FMNH 204363/1; WA-513, Ivy Tank Cave (N-161), FMNH 204351/50; Ivy Tank, RNHL/50+; WA-511, Murrawijini Cave # 1 (N-7), NNW of Nullarbor, FMNH 204345/n; WA-517, wombat infested doline (N-122), W of Nullarbor Roadhouse, FMNH 204370/90; WA-519, doline (N-163) NW of Nullarbor, FMNH 204305/2, FMNH 204306/n; WA-507, Giants Head Cave (N-16), SSE of Koonalda, FMNH 204305/2, FMNH 204306/n; WA-507, Giants Head Cave (N-178), N of Koonalda, FMNH 204313/2; WA-520, doline (N-148) WNW of Nullarbor, FMNH 204383/12; WA-509,700 metres WNW of Wigunda microwave tower, FMNH 204332/2; WA-504, Allen's Cave (N-145), SSE of Sixteen Mile Tank, FMNH 204300/n; WA-522, Wilson's Bluff, FMNH 204396/76].

Western Australia: Nullarbor Plain [WA-498, Eucla Pass crest, FMNH 204241/1; WA-499, Weebubbie Cave (N-2), WNW of Eucla, FMNH 204249/30, FMNH 204252/9; WA-528, side of scarp, WSW of Eucla, FMNH 204436/5; WA-527, Najoda Rock Hole, E of Eucla, FMNH 204429/1, FMNH 204430/6; Eucla, RNHL/25+; WA-503, Winbirra Cave (N-45), W of Eucla, FMNH 204289/28; WA-

502, Kutowalla doline (N-44), W of Eucla, FMNH 204272/1; WA-500, rim of Chowilla Landslip (N-17), WNW of Eucla, FMNH 204260/21; WA-526, halfway up scarp, Knousley Tank, NE Hearder Tower, W of Eucla, FMNH 204424/51; WA-525, scarp base, W of Yakcoorga Rock Hole, E of Mundrabilla, FMNH 204412/5, FMNH 204413/1; Witches Cave, Mundrabilla, 21 May 1985, WAM 170.86/16; WA-524, Kuthala Pass, N of Mundrabilla Roadhouse, FMNH 204430/2; WA-530, 92.4 km N of Mundrabilla Homestead, Forrest track, FMNH 204438/36; WA-531, 5 km S of Forrest, Mundrabilla track, FMNH 204444/8; WA-533, 29 km S of Forrest, Mundrabilla track, FMNH 204453/ 39; WA-497, near Mundrabilla microwave tower, FMNH 204220/1, FMNH 204227/12; WA-532, Old Homestead Cave (N-83), 39 km S of Forrest, Mundrabilla track, FMNH 204451/2, FMNH 204452/ 76; WA-529, Forrest track, 31.8 km N of Mundrabilla, FMNH 204441/2, FMNH 204442/29; WA-534, 9.8 km N of scarp edge, Forrest track from Mundrabilla, FMNH 204457/2; WA-535, base of scarp, gully just above Mundrabilla Homestead, FMNH 204464/1; WA-536, Roe Plains, 10.6 km S of Eyre Highway, E of Madura, FMNH 204470/6; 25 miles E of Madura, RNHL/2; WA-537, Moodini Pass, E of Madura, FMNH 204478/32; WA-494, Madura 6 Mile South Cave (N-62), S of Madura, FMNH 204206/7; 8 miles W of Loongana, RR line, WAM 117.86.5; WA-495, E side of crest, Madura Pass, FMNH 204215/1; WA-538, Dingo Donga Cave (N-160), WNW of Madura, FMNH 204495/ 51, FMNH 204496/6; WA-493, 360 metres N of Eyre Highway, W of Madura, FMNH 204195/95; FMNH 204197/1; WA-491 cave (N-91), Cocklebiddy, FMNH 204188/2; WA-490B, Cocklebiddy Cave, FMNH 204177/1; WA-490A, Cocklebiddy Cave, FMNH 204172/60, FMNH 204173/3; Cocklebiddy Cave, 14 May 1985, WAM 169.86/1; Caiguna, RNHL/30+; Cardanumbi (AM C.63669, syntypes of Themapupa beltiana contexta Iredale, 1939); WA-488, scrub behind John Eyre Motel, Caiguna, FMNH 204155/16, FMNH 204156/7; WA-539, 33.4 km W of John Eyre Motel, FMNH 204497/8; WA-489, 5.9 km E of Caiguna, FMNH 204164/2; 70 miles NE of Rawlinna, RR line, 9 February 1969, WAM 102.86/11, 26 January 1969, WAM 139.86/n; 85 miles NE of Rawlinna, 9 February 1969, M. Thomas!, WAM/n; 54 km E of Balladonia, 12 May 1985, WAM 171.86/2, WAM 172.86/3; WA-541, 38.3 km E of Balladonia, FMNH 204521/9]; Balladonia-Norseman-Esperance area (12 miles WNW of Naretha, RR line, 21 March 1971, WAM 110.86/9; WA-94, WA-487, scrub behind Balladonia Roadhouse, FMNH 182263/n, FMNH 182445/3, FMNH 204139/1; Balladonia, RNHL/7, RNHL/59+; WA-543, Juranda Rock Hole, Balladonia-Cape Arid track, FMNH 204547/2, FMNH 204548/3; Juranda Rock Hole, 2 October 1976, WAM 119.86/1; Pine Hill, S of Balladonia, WAM 120.86/2, WAM 121.86/1; 15 miles SW of Balladonia, WAM 118.86/3; WA-544, E side Juranda Rock Hole, FMNH 204560/1; 60.3 miles S of Balladonia, 8 November 1966, WAM 116.86/2; 18 km NE Charlina Rocks, 15 October 1977, WAM 1246.81/4; WA-95, Afghan Rock, near Balladonia, FMNH 182281/ 1; WA-486, 7.5 km ENE of Newman Rock, FMNH 204126/1; WA-93, 51 miles E of Norseman, FMNH 182274/n; WA-91, Cape Le Grand Road, FMNH 182428/1; Buldania, 12 February 1980, WAM 179.86/ 3; 30 km NNE of Norseman, 6 March 1980, WAM 175.86/3, WAM 176.86/13; 10 miles N of Norseman, Lake Cowen, 7 March 1980, WAM 174.86/7; Grass Patch, WAM 93.86/6, WAM 94.86/ 8, WAM 95.86/1; WAM 638.76/3; Samphire Flats, SE corner of Fitzgerald, 14 February 1977, WAM 177.86/21; Peak Charles, WAM 632.76/2, WAM 634.76/2 WAM 635.76/4, WAM 636.76/n, WAM 637.76/n, WAM 639.76/1, WAM 640.76/17, WAM 641.76/1, WAM 646.76/2, WAM 660.76/1, WAM 109.86/2; 5 km S of Peak Eleanora, 8 November 1979, WAM 114.86/1; 1 mile WNW of Peak Eleanora, 17-18 January 1977, WAM 1267.81/1; Ponton Creek or Goddard's Creek, Boondaroo Station, 18 August 1967, WAM 112.86/14); Kalgoorlie area (Fox's Find, 33.4 km from Kambalda, 16 February 1980, WAM 180.86/2; NE side Mt. Shea, 20 km SSE of Kalgoorlie, 15 March 1981, WAM 182.86/ 19, WAM 188.86/24; 3 km SE Southern Cross, 19 March 1980, WAM 184.86/1; 5 km S of Yellowdine, 21 March 1980, WAM 178.86/1): Bremer Bay region (Boat Harbour, Beaufort Inlet, W of Bremer Bay, 10 October 1974, WAM 106.86/11; 22 km W of Jerdacuttup, 17 November 1976, WAM 130.84); Merredin area (WA-98, Nangeenan townsite reserve, near Merredin, FMNH 182221/n, FMNH 200491/4; Nangeenan, E. Sedgwick!, AM C.64861, AM C.64898, paratypes of Themapupa beltiana asserta Iredale, 1939; Nangeenan townsite reserve, 10 November 1968, WAM 8.69/n; Holleton, September 1977, WAM 91.86/1; Gibb Rock via Narembeen, May 1971, WAM 113.86/1; WA-99, Hines Hill townsite reserve, FMNH 182257/1; Hines Hill townsite reserve, 10 November 1968, WAM 129.84/n); NE of Perth (government reserve 10 miles E of Nugadong, 14 July 1975, WAM 105.86/ 4; Morawa, 6 June 1976, WAM 92.86/1).

#### Range

Pupoides adelaidae (Adams & Angas, 1864) is the common pupillid between Hines Hill near

Merredin and Nundroo in South Australia. It has not been found in the Albany area. There are several records from the transcontinental rail line in Western Australia, plus an inland extension to 85 miles NE of Rawlinna. Collections at Morawa (29° 13' S, 116° 00' E) and near Nugadong (30° 12' S, 116° 39' E), NNE of Perth bring the total range near to the west coast. In view of the limited collecting from this area, further extensions are probable. Published records from the Eyre Peninsula to Victoria (Gabriel, 1930) are too limited for range delineation, but it is common on the Eyre Peninsula and in the Flinders Ranges (Solem, in preparation).

#### Discussion

This is the only pupilloid known to extend through the northern part of the wheat belt area to near the west coast at Morawa and Nugadong, although *Pupilla australis* (Adams & Angas, 1864) has off shore island records (Rottnest and Houtman Abrolhos). *Pupoides adelaidae* (Adams & Angas, 1864) has not been found on islands in the Recherche Archipelago and does not reach the Albany area inhabited by other pupilloids.

The several records along the transcontinental railroad compare with the few Forrest track records for other species. This may be caused, in part, by the larger size and generally greater abundance of *P. adelaidae*. The casual searcher would notice this species first and possibly mistake the smaller sized taxa as juveniles and not bother to collect them.

No trends in size among populations could be detected. Both large and small individuals were found inland and along the coast. Kangaroo Island, SA and Hines Hill, WA populations could not be separated on shell features. Thus the proposal of Iredale (1939:11) to give subspecific status to populations from Nangeenan in the wheat belt (*assertus*) and the Nullarbor Plain (*contextus*) are rejected.

## Pupoides lepidulus (Adams & Angas, 1864)

(Fig. 34)

Buliminus (Chondrula) lepidula Adams & Angas, 1864, Proc. Zool. Soc. London, 1864:38 — Shark Bay, Western Australia.

Bulimus lepidula (Adams & Angas), Cox 1868, Monog. of Aust. Land Shells, p. 69, pl. 19, figs 14, 14a, 14b.

Bulimus pacificus E.A. Smith, 1874 (not Pfeiffer, 1846) Zool. Erebus & Terror, Mollusca, p. 3, pl. IV, fig. 6 — Pigeon Island, NW Australia.

Pupa lepidula (Adams & Angas), E.A. Smith, 1894, Proc. Malc. Soc. London, 1 (3):96

Pupoides lepidulus (Adams & Angas), Hedley, 1916, Jour. Roy. Soc. Western Aust., 1:68.

Pupoides pacificus (Pfeiffer), Pilsbry, 1921, Man. Conch., (2) 26:141-144 - In part.

Themapupa lepidula (Adams & Angas), 1937, Aust. Zool., 8 (4):303-304; Iredale, 1939, Jour. Roy. Soc, Western Aust., 25:10, pl. 1, figs 5, 5a.

## **Comparative remarks**

Pupoides lepidulus (Adams & Angas, 1864) is by far the smallest of the Western Australian species, shell height 4.05-4.64 mm (mean 4.37 mm), and has dextral coiling, strongly rounded whorls and a tapering spire (Fig. 34). *P. ischnus* (Tate, 1894) from the Red Centre is the same size, shell height 3.92-4.77 mm (mean 4.26 mm), but the shell is slenderer and sinistral in coiling (Fig. 29). *Pupoides beltianus* (Tate, 1864) from the Red Centre (Figs 35-36) is larger (shell height 3.66-5.13 mm, mean 4.22 mm), has a more obese shell, dextral coiling, and the whorl sides are flatter. West coast specimens that may be this species (see below) are slightly larger than *P. lepidulus*, shell height 4.31-5.10 mm (mean 4.73 mm).

#### Material

Western Australia: Broome (Looroo Well, Cape Latouche-Treville, 4 June 1943, C. Davis!, AM/ 3); Pilbara Wyloo Station, Log Hut, 29 August 1969, WAM 96.86/1; WA-42, limestone reef, 1 mile S of Port Hedland, FMNH 182607/10); North West Cape (WA-172, 1.4 km N of 4 Mile Well, Ningaloo-Cardabia Road, FMNH 200336/2; Cy Creek, Cardabia, 6 April 1969, T. Darragh & G.W. Kendrick!, WAM 126.86/n, FMNH 215137/5; South Muiron Island, 11 June 1970, W.K. Youngson!, WAM/1); Barrow Island (9 January 1973, H. Butler!, WAM/4); Dampier (WAM/1); Carnarvon area (WA-168, Ram Paddock Well, Quobba Station, FMNH 200335/4): Houtman Abrolhos (Pigeon Island, close to Wallaby Island, Dr. Richardson!, BMNH 44.12.11.64).

### Range

The type locality of Shark Bay is accepted as accurate, although I have not seen any examples from there that match the specimens listed above. The confirmed range is from Houtman Abrolhos to Cape Latouche-Treville, with one inland record from Wyloo Station, Pilbara.

## Discussion<sup>\*</sup>

The original figure of *Pupoides lepidulus* (Adams & Angas, 1864) is distorted. The cited dimension of "2 lines", equivalent to 4.22 mm, and slender form are sufficient to suggest that this name be used in this context. Only the Cy Creek sample contained many individuals. They are dwarfed, shell height of 32 adults is 3.14-3.92 mm (mean 3.60 mm), compared with a mean and range of 4.37 mm (4.05-4.64 mm) for ten adults from the other stations. Similar dwarf examples of *Pupoides contrarius* (E.A. Smith, 1894) and *Pupoides* aff. *beltianus* also were found at Cy Creek.

## Pupoides aff. beltianus (Tate, 1894)

(Fig. 36)

#### **Comparative remarks**

The populations grouped here may prove to belong to the Red Centre species *Pupoides beltianus* (Tate, 1894). The shell morphology is nearly identical (Figs 35-36), but material available is too limited to make a firm decision. The specimens are of medium size, shell height 4.31-5.10 mm (mean 4.73 mm), which is almost the same as the morph referred to as *P*. aff. adelaidae (Fig. 32), which has a shell height of 4.38-5.36 mm (mean 4.87 mm) and flatter sided whorls. *P. lepidulus* (Adams & Angas, 1864) differs in its much more slender shape (Fig. 34) and smaller size (shell height 4.05-4.64 mm, mean 4.37 mm). The sinistral coiling of *P. contrarius* (E.A. Smith, 1894) immediately separates that species (Fig. 27).

#### Material

Western Australia: Pilbara (Dale's Gorge, Hamersley Range, 31 August 1975, WAM 98.86/1, WAM 107.86/7; North West Cape (main road, WAM 99.86/1; Cy Creek, Cardabia Station, 6 April 1969, T. Darragh & G.W. Kendrick!, WAM 132.84/n, FMNH 215138/5); Warroora Station (WA-955, coastal dunes, FMNH 212477/1; 29 June 1972, N. Coleman!, 1, AM/10); Shark Bay (Wooramel Cliff, 7 November 1977, WAM 136.86/1; Useless Loop, WAM 140.86/11, WAM 66.673/3; Hamelin Pool Station, 2 March 1966, WAM 101.86/2; South Passage, 5 March 1966, WAM 111.86/2; 4 miles W of Tamala Homestead, 8 March 1966, WAM 124.86/18; Yaringa Station, 26 June 1982, WAM 83.2868; WA-165, near Overlander Roadhouse, FMNH 199646/1).

## Discussion

The more rounded whorls (Fig. 36) of *Pupoides* aff. *beltianus* (Tate, 1894) are the only feature clearly distinguishing this morph from *P.* aff. *adelaidae* (Adams & Angas, 1864) (Figs 32-33). In view of the limited material, mosaic distribution pattern, and complete lack of any anatomical specimens, it seems best to indicate tentative affinities for these, rather than to make firm assignments.

As in *Pupoides lepidulus* (Adams & Angas, 1864), and *P. contrarius* (E.A. Smith, 1894) specimens from Cy Creek, Cardabia Station were dwarfed. Comparative measurements follow:

		MEAN AND RANGE OF
LOCALITY	SPECIMENS	HEIGHT IN MM
Other	24	4.73 (4.31-5.10)
Cy Creek	25	4.26 (3.79-4.97)

Since two other pupillids from the same station, *Gastrocopta deserti* Pilsbry, 1917 and *G. pilbarana*, new species, showed no diminution in size, there is obvious potential for field studies.

## Pupoides aff. adelaidae (Adams & Angas, 1864)

(Figs 32-33)

#### **Comparative remarks**

The flatter sides to the spire whorls (Fig. 32) and slight difference in whorl width agree better with the south coast *Pupoides adelaidae* (Adams & Angas, 1864) than with any of the west coast

species. The morph referred to above as *Pupoides* aff. *beltianus* (Tate, 1894) differs in the more rounded and slightly narrower whorls (Fig. 36). Differences in size are negligible. The very slender (Fig. 34) and much smaller *P. lepidulus* (Adams & Angas, 1894) and the sinistral *P. contrarius* (E.A. Smith, 1894) (Fig. 27) are easily differentiated.

#### Material

Western Australia: Warroora Station (limestone ridge with *Ficus*, 5 June 1981, WAM 1453.81/ 8); Carnarvon area (WA-167a, depression near lighthouse, Point Quobba, FMNH 200356/16); Shark Bay (WA-1, 059, gully W of Great Northern Highway, 2.5 km N of 26th Parallel marker, FMNH 211989/1; N of Shark Bay turnoff, Great Northern Highway, 9 September 1975, WAM 123.86/4; ½ mile west of 512 mile peg, Great Northern Highway, NNE of Carbla Homestead, near Hamelin Pool, 20 August 1968, WAM 134.86/9).

#### Discussion

Whether this is a growth phase of *Pupoides* aff. *beltianus* associated with limestone or a distinct species is unknown. Additional field work is needed.

## DISCUSSION AND BIOGEOGRAPHY

The 11 species or probable species reviewed above present several problems for further investigation. All of these species aestivate by sealing to an object. This may be a rock, a bit of broken leaf, a piece of bark, a pebble, or another shell. The epiphragms are mucoid, without evident calcareous thickening. Remnants of such a seal are shown in *Gastrocopta pilbarana* (Figs 16-18). It is a very thin sheet attaching the outer rim of the aperture to the object. This epiphragm is not water soluble. No information is available as to its chemical structure.

Most specimens were collected dead, sorted out of dirt or litter. Adherent particles within the apertures (Figs, 2, 4, 6-7, 9, 10, 12, 14-15, 20) are clear indicators of dead material. Most living or freshly dead specimens had encrustations on the shell surface. These proved almost impossible to remove, even with detergents and a sonic cleaner, and presumably are part of natural coverings.

Future field work should involve maximum efforts to collect live specimens from their hidden pockets of rubble or litter. Because of the small size and often complex apertural barriers, pupilloids are prime candidates for accidental distribution by floods. A bubble of air trapped inside the spire provides buoyancy. Dead specimens can be carried for many kilometres, and even live examples sealed to a bit of bark or leaf can be carried for an equal distance. Collections from stream side debris only indicate that the species lives (or lived) upstream, not that it exists at this place now. Similarly, bleached shells on open ground can be the leavings of floods, weathered out from Holocene deposits, or from a nearby colony. Particularly with all the changes brought on by pastoral and farming activities, it will be necessary to seek live material to establish actual presence, or at least to determine if dead examples came from a restricted slope or gully, or could have been transported from 100 or more kilometres away.

A second unusual aspect to these species is the number of shell layers deposited on the apertural lips (Figs 2, 4, 6, 7, 12, 14, 17, 20, 22, 23, 26, 28, 38-36). In some examples there are clear indications of many layers, in others this is not obvious. If the additional layers do not extend to the edge of the previous one, then the separate layers are obvious. But if the last layer is extended to the lip edge itself (see Figs 7, 9, 14, 15, 17, etc.), then a cross-sectional fracture would be required to gain an estimate of layer numbers. Possibly these layers may involve responses to local weather conditions, *i.e.*, a new layer added after a "good" local rain event and subsequent extended activity period. If they could be established as *seasonal* rather than *opportunistic* depositions, then they might be used to determine specimen age. Certainly the number of layers seen suggests a fairly extended life span, since most of the figured specimens come from areas of both low and infrequent rainfall. Controlled laboratory experiments involving periods of activation and aestivation will be required to work out the pattern of such depositions.

## Biogeography

The first constraint on interpreting the distribution records is the area actually collected. The second constraint is the experience of the collector. Whereas an experienced and dedicated

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"snailer" would use the sign of a few bleached "bones" as the incentive to hunt for "good, live examples" or the sight of a stream drift deposit to grab a bag full of debris for later sorting, thus increasing greatly the chance of picking up rare snails (0.1-1% of snails present), the "casual traveller" interested in vertebrates will pick a few from the surface and hurry to the next rock that might conceal a lizard, ignoring the aestivating micro-mollusks sealed to the rock itself.

Sufficient collecting has been done in the area from Perth south to Cape Leeuwin and then west to Albany, that the absence of pupilloids from this part of Western Australia seems certain. They have not been found in the wetter forests of the Porongurup and Stirling Ranges NE of Albany, despite fairly intensive collecting. The western limits of species that occur near Peak Eleanora and Peak Charles, and the south coast Albany-Bremer Bay-Esperance records probably are reasonably accurate indicator points. From Norseman, WA east to Nundroo, SA, collecting has been comprehensive in a transect of a few kilometres on either side of the Eyre Highway. I have made a single collecting transect north from Mundrabilla to Forrest on the transcontinental railroad line. There are a few casual collections near other sidings on the railroad for *Pupoides adelaidae* (Adams & Angas, 1864), and one record from 85 miles NE of Rawlinna, but the area north of the Eyre Highway from Nundroo west to Kalgoorlie, WA, and then NNW to Paynes Find in the gold fields, west to Morawa, and north to near Geraldton has had virtually no collecting effort. The current western limits from townsite reserves at Hines Hill and Nangeenan near Merredin in the wheat belt probably are lack of collecting artifacts.

In South Australia, there are gaps of almost no collecting from 14 miles E of Nundroo NE to the Gawler Ranges, and also from Nundroo SE to about the level of Venus Bay on the Eyre Peninsula. Collections from some of the Eyre Peninsula, Yorke Peninsula, Flinders Ranges, and Kangaroo Island have yielded pupilloids, but they are not a prominent part of the fauna. In the Musgrave and Mann Ranges and then north through most of the Red Centre, pupilloids are common and diverse (Solem, In preparation). There are only a few records from the Warburton-Rawlinson area, and no land snails have been sought for in the area between Warburton and the Pilbara.

Collecting effort along the west coast has been sporadic, with the area from Geraldton to Port Hedland covered fairly well along the Great Northern Highway, much less extensively inland. Many of the records from this area are by non-malacologists, and much remains to be learned about distributions and speciation in this area.

Given the above outline of imperfect knowledge, a few positive conclusions can be drawn.

Several species share a rough Nundroo, SA to Albany and Hines Hill near Merredin, WA range, then recur in the Eyre Peninsula-Kangaroo Island-Murray River region, but with some individual aspects:

*Gastrocopta margaretae* (Cox, 1868) reaches Albany, Kalgoorlie, and Nangeenan, was collected at three stations along the Forrest track, thus demonstrating some inland penetration, and reached the Nuyts and Recherche Archipelago.

Pupilla (Gibbulinopsis) australis (Adams & Angas, 1864) also extends Nundroo to Albany, has only one record significantly north of the Eyre Highway (42 miles S from Xanthus), and has been recorded west of the Norseman-Peak Eleanora axis inland only once, at Hines Hill. It has not been taken on the Recherche Archipelago. There are then the surprising records from Rottnest Island off Perth, Houtman Abrolhos off Geraldton, and on the mainland at Point Quobba, N of Carnarvon and Green Head, near Eneabba.

*Pupoides myoporinae* (Tate, 1880) occurs at scattered sites from Yalata, SA to Norseman, Kalgoorlie, and Hines Hill near Merredin. It has not been collected north of the railroad, or south of Peak Charles. It has not been found in the Esperance to Albany coastal area, or on the off shore islands.

*Pupoides adelaidae* (Adams & Angas, 1864) extends west along the coast only to the Bremer Bay area, then Hines Hill in the wheat belt. There are numerous records along the transcontinental railroad, plus the records near Morawa and Nugadong, NNE of Perth. It usually is the most abundant species present, and occurs in more exposed micro-habitats than the other species.

The above differences in western extensions offer many opportunities for field studies to refine range limits, determine if micro-sympatry or niche specialization occurs, and investigate the vast uncollected inland areas. Certainly *Gastrocopta margaretae, Pupilla australis,* and *Pupoides adelaidae* probably will be found to have inland range extensions.

Along the west coast, fewer records mean greater collecting gaps and less certainty as to actual range limits. Inland records are almost absent. Certainly *Gastrocopta deserti* Pilsbry, 1917, *Gastrocopta wallabyensis* (E.A. Smith, 1894) as a probable close relative of *G. tatei* Pilsbry, 1917, and *Pupoides* aff. *beltianus* (Tate, 1894), as actual or close relatives of Red Centre taxa, are prime candidates for inland range extensions. The current known limits probably have little meaning, but are summarized below.

Gastrocopta wallabyensis (E.A. Smith, 1894)

Point Quobba S to Green Head (30° 04' S, 114° 58' E)

Gastrocopta deserti Pilsbry, 1917

Cy Creek on Cardabia Station, Barrow Island, Dampier Archipelago, and Point Quobba Gastrocopta pilbarana, new species

Roy Hill south through Shark Bay

Pupilla australis (Adams & Angas, 1864)

Point Quobba, Houtman Abrolhos, Green Head, Rottnest Island

Pupoides contrarius (E.A. Smith, 1894)

Cape Latouche-Treville and Pardoo, Pilbara south to Shark Bay and Houtman Abrolhos Pupoides lepidulus (Adams & Angas, 1864)

Cape Latouche-Treville south through Shark Bay to Houtman Albrolhos

Pupoides aff. beltianus (Tate, 1894)

Dale's Gorge, Hamersley south through Shark Bay

Pupoides aff. adelaidae (Adams & Angas, 1864)

North West Cape south through Shark Bay

The potential Red Centre taxa (*deserti, wallabyensis* and *beltianus*) are supplemented by more southern species (aff. *adelaidae, australis*). It is not possible, at this time, to suggest derivations for the other taxa.

Two associations of species suggest field projects. At Point Quobba (WA-167a), *Gastrocopta wallabyensis, G. deserti, Pupilla australis, Pupoides contrarius,* and *Pupoides* aff. *adelaidae* have been collected from the same clump of shrubs. None of the species appear unusual. At Cy Creek, Cardabia Station, just south of the Cape Range, a different set of five species were taken from a drift deposit. *Gastrocopta deserti and G. pilbarana* were normal in size, but the examples of *Pupoides contrarius, P. lepidulus,* and *P. aff. beltianus* were dwarfed. Point Quobba is favourably situated in terms of sea mists and is a good molluscan habitat. Cy Creek, in contrast, is drier than the Cape Range and would rank as a harsher habitat. Why some species are dwarfed at the latter locality and some retain normal adult size is another project for future investigation.

## LITERATURE CITED

- Adams, A.A. and Angas, G.F. 1864a. On the Land-Shells of South Australia. Proc. Zool. Soc., London 1863:519-523.
- - - 1864b. Descriptions of New Species of Shélls, chiefly from Australia, in the Collection of Mr. Angas. Proc. Zool. Soc., London 1864:35-40.

Cox, J.C. 1868. A monograph of Australian land shells. William Maddock, Sydney. 111 pp., 20 pls.

Gabriel, C.J. 1930. Catalogue of the Land Shells of Victoria. Proc. Roy. Soc. Victoria 43 (1):62-88, pls 2-3.

- - - - - 1947. Additions to and alterations in the catalogue of the land shells of Victoria (including descriptions of new species). Mem. National Mus. Victoria 15:109-125, pls 9-10.

Hedley, C. 1916. A Preliminary Index of the Mollusca of Western Australia. Jour. Roy. Soc. Western Aust. 1 (1914-1915):1-77.

## 118 A. Solem

Iredale, T. 1930. Notes on some Desert Snails. Victorian Nat. 47 (7):118-120, fig. 1

---- 1937a. A Basic List of the Land Mollusca of Australia. Aust. Zool. 8 (4):287-333.

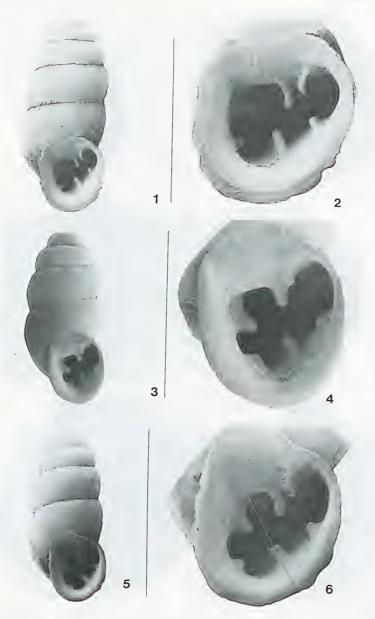
- ---- 1937b. An Annotated Check List of the Land Shells of South and Central Australia. South Aust, Nat. 18 (2):6-57, pls 1-2, map.
- - - 1939. A Review of the Land Mollusca of Western Australia. Jour. Roy. Soc. Western Aust. 25:1-88, pls 1-5, map.

Pilsbry, H.A. 1916-1918. Manual of Conchology (2) 24:i-xii, 1-380, figs 1-18, pls 1-49.

- ---- 1920-1921. Manual of Conchology (2) 26:i-iv, 1-254, figs 1-4, pls 1-24.
- ---- 1927-1935. Manual of Conchology (2) 28:i-xii, 1-226, figs 1-12, pls 1-31.
- - - 1948. Land Mollusca of North America (North of Mexico). Acad. Nat. Sci., Philadelphia, Monogr. 3, 2 (2): i-xlvii, 521-1113, figs 282-585.
- Rousseau, D.D. and Laurin, B. 1984. Variations de Pupilla muscorum L. (Gastropoda) dans le quaternaire d'Achenheim (Alsace): une analyse de l'interaction entre espece et milieu. Geobios, Mem. special no. 8:349-355, figs 1-7.
- Smith, B.J. and Kershaw R.C. 1979. Field guide to the non-marine molluscs of South Eastern Australia. Australian National University Press, Canberra. 285 pp., 115 maps, text figs.
- Smith, E.A. 1894. On the Land-Shells of Western Australia. Proc. Malac. Soc. London 1 (3):84-99, pl. 1, figs 8-32.
- Solem, A. 1981. Small Land Snails from Northern Australia, I: Species of Gyliotrachela Tomlin, 1930 (Mollusca: Pulmonata; Vertiginidae). Jour. Malac. Soc. Australia 5 (1-2):87-100, figs 1-19.
- ----- In Preparation. Non-camaenid Land Snails of the Kimberley and Northern Territory, Australia. Part I. Systematics, affinities, and ranges.
- Tate, R. 1894. Brief Diagnoses of Mollusca from Central Australia. Trans. Roy. Soc. S. Australia 18:191-194.
- ----- 1896. Mollusca. In: Report Horn Scientific Expedition to Central Australia, Part II. Zoology:181-226, figs A-P, pls 17-19.
- Zilch, A. 1959-1960. Gastropoda Euthyneura. Lief. 1-4. Handbuch der Paläozoologie 6 (2):1-834, figs 1-2, 515.

## Addendum

Numerous Nullarbor pupilloids are in the SAM and WAM collections. These were examined after submission of the manuscript. Significant range extensions were incorporated, but "fill-in" cave records or duplicated records were not added.



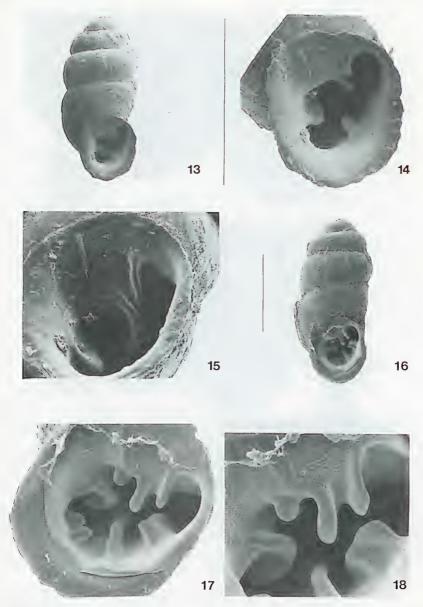
## FIGURES 1-6

Shells of *Gastrocopta margaretae* (Cox, 1868): 1-2, topotype of *Australbinula complexa* Iredale, 1939, Nangeenan, near Merredin, WA, 17 April 1977, FMNH 200490, 1 — whole shell, 2 — aperture; 3-6, WA-516, 2 km E of Yalata turnoff, SE of Yalata Roadhouse, Nullarbor Plain, SA, 10 June 1979, FMNH 204365, 3-4, specimen with reduced angular barrier, 5-6, specimen with large, sinuated angular barrier. Scale lines equal 1 mm.



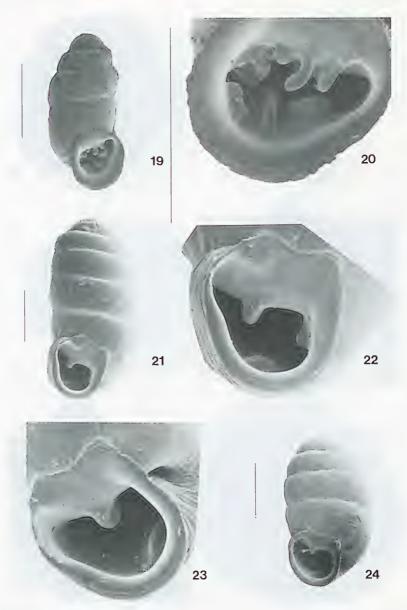
## FIGURES 7-12

Shells of *Gastrocopta margaretae* (Cox, 1868) and *Gastrocopta wallabyensis* (E.A. Smith, 1894): 7-10 *G. margaretae*, 7, WA-516, 2 km E of Yalata turnoff, S of Yalata Roadhouse, Nullarbor Plain, SA, 10 June 1979, FMNH 204365, specimen with large, simple angular barrier, 8-9, lectotype of *Pupa margaretae* Cox, 1868, Wallaroo, Yorke Peninsula, SA, SMF 55236, 10, paratype of *Bifidaria bannertonensis* Gabriel, 1930, Bannerton, Murray River basin, Victoria, FMNH 117024 ex C.J. Gabriel; 11-12, *G. wallabyensis*, WA-167a, depression near lighthouse, Point Quobba, N of Carnarvon, WA, 16 April 1977, FMNH 200358. Scale lines equal 1 mm.



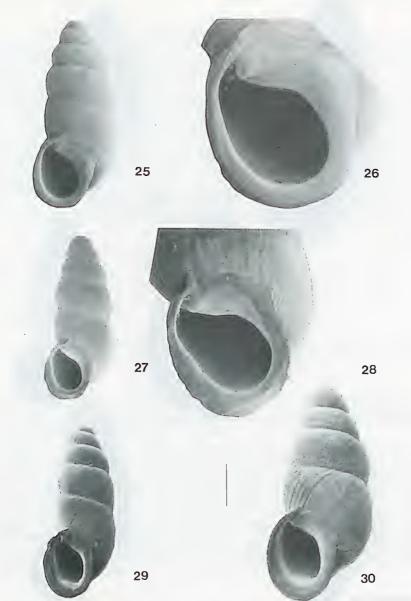
## FIGURES 13-18

Shells of *Gastrocopta deserti* Pilsbry, 1917 and *Gastrocopta pilbarana*, new species: 13-15, *G. deserti*, WA-167a, depression near lighthouse, Point Quobba, N of Carnarvon, WA, 16 April 1977, FMNH 201611, 13, whole shell, 14, aperture, 15, vertical view of parietal, angular, and columellar barriers; 16-18, *G. pilbarana*, new species, holotype, Sandy Point, Dirk Hartog Island, Shark Bay, WA, 29 April 1974, WAM 127.84, 16 — whole shell, 17 — aperture with epiphragm remnants, 18 — detail of barriers. Scale lines equal 1 mm.



FIGURES 19-24

Shells of *Gastrocopta pilbarana*, new species and *Pupilla (Gibbulinopsis) australis* (Adams & Angas, 1864): 19-20, *G. pilbarana*, paratopotype, Sandy Point, Dirk Hartog Island, Shark Bay, WA, 29 April 1974, WAM 145.86, 19 — whole shell, 20 — aperture showing mature basal and upper palatal barriers; 21-24, *P. (G.) australis*, Bathurst Point, Rottnest Island, WA, December 1973, WAM 161.86/2, 21 — whole shell, 22 — detail of aperture, 23 — angled view of angular node and barriers, 24 — smaller adult with newly reflected lip and small barriers. Scale lines equal 1 mm.



## FIGURES 25-30

Shells of *Pupoides myoporinae* (Tate, 1880) *P. contrarius* (E.A. Smith, 1894), *P. ischnus* (Tate, 1894), and *P. eremicolus* (Tate, 1894): 25-26, *P. myoporinae*, WA-516, 2 km E of Yalata turnoff, Nullarbor Plain, SA, FMNH 204364, 25 — whole shell, 26 — aperture; 27-28, *P. contrarius*, WA-167a depression near lighthouse, Point Quobba, N of Carnarvon, WA, FMNH 200357, 27 — whole shell, 28 — aperture; 29, *P. ischnus* (Tate, 1894), Central Australia, FMNH 102333, probably cotypes, FMNH 102333, whole shell; 30, *P. eremicolus*, Inkamulla, Harts Range, Red Centre, FMNH 198925, whole shell. Scale lines equal 1 mm.



Shells of Pupoides adelaidae (Adams & Angas, 1864), P. aff. adelaidae, P. lepidulus (Adams & Angas, 1864), P. aff. beltianus, and P. beltianus (Tate, 1894): 31, P. adelaidae, WA-93, salt pan by Eyre Highway, 51 miles E of Norseman town centre, WA, FMNH 182275, whole shell; 32-33, P. aff. adelaidae, WA-167a, depression near lighthouse, Point Quobba, N of Carnarvon, WA, FMNH 200356, 32 - whole shell, 33 - aperture; 34, P. lepidulus, WA-42, 1 mile S of Port Hedland, FMNH 182607, whole shell; 35, P. beltianus, Illamurta Springs, James Range, Red Centre, FMNH 198784, whole shell; 36, P. aff. beltianus, Dale's Gorge, Hamersley Range, Pilbara, WA, WAM 107.86, whole shell. Scale lines equal 1 mm.